









# **Bulletin** *of the* **Torrey Botanical Club**

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## CONTENTS

Vaccinium Hybrids and the Development of New Horticultural Material <i>George M. Darrow and W. H. Camp</i>	1
Dryopteris, Deschampsia, Portulaca, Lupinus, Fagara, Stenogyne, and Dubautia. Hawaiian Plant Studies 12 . . . . . <i>Harold St. John</i>	22
The Jatrophas of Cervantes and of the Sessé & Mociño Herbarium. <i>Rogers McVaugh</i>	31
Juniperus virginiana, J. horizontalis, and J. scopulorum—III. Possible Hybridization of J. horizontalis and J. scopulorum. <i>Norman C. Fassett</i>	42
Rhizidiomyces hirsutus Sp. Nov., a Hairy Anisochytrid from Brazil. <i>John S. Karling</i>	47
History and Nomenclature of the Higher Units of Classification. <i>Leon Croizat</i>	52
Effect of Cotton on the Germination of Phycomyces Spores. <i>William J. Robbins and Mary Bartley Schmitt</i>	76
A Morphological and Cytological Study of a New Form of Volvox—I. <i>Jerome Metzner</i>	86
Index to American Botanical Literature . . . . .	114
A Morphological and Cytological Study of a New Form of Volvox—II. <i>Jerome Metzner</i>	121
The Anatomy of Peach and Cherry Phloem . . . . . <i>Henry Schneider</i>	137
Further Studies on the Antibiotic Activity of Lichens. <i>Paul R. Burkholder and Alexander W. Evans</i>	157
A Survey of Some Wood-destroying and Other Fungi for Anti-bacterial Activity. <i>William J. Robbins, Annette Hervey, Ross W. Davidson, Roberta Ma and William C. Robbins</i>	165
Studies in the Sapotaceae—I. The North American Species of Chrys- sophyllum . . . . . <i>Arthur Cronquist</i>	191
Descriptions of Tropical Rusts—VII . . . . . <i>George B. Cummins</i>	205
New Combinations in Cornus . . . . . <i>H. W. Rickett</i>	223
Index to American Botanical Literature . . . . .	224
Estimates of the Minimum Numbers of Genes Differentiating Several Taxonomic Categories in the Genus Solidago . . <i>Richard H. Goodwin</i>	235
The Validity of the Algal Genus Thamniastrum . . . <i>Clarence E. Taft</i>	246
Thomas Jefferson. His Interest in Plant Life as Revealed in His Writ- ings—II . . . . . <i>Edmund H. Fulling</i>	248
The Genus Jatropha in America: Principal Intrageneric Groups. <i>Rogers McVaugh</i>	271

A Report of Some Recent Collections of Rubiaceae from Ecuador.	
	<i>William Campbell Steere</i> 295
"Euphorbia Chamaesyce" in the United States .....	<i>Leon Croizat</i> 312
The Genus <i>Cnidoscopus</i> in Mexico: New Species and Critical Notes.	
	<i>Cyrus Longworth Lundell</i> 319
Index to American Botanical Literature .....	335
Glandular Leaf Hairs of Oriental Tobacco.	
	<i>Nancy J. Bentley and F. A. Wolf</i> 345
Cytoplasmic Hybrids in <i>Penicillium notatum</i> .	
	<i>Carl C. Lindegren and Henry N. Andrews</i> 361
Chromosomes of Cruciferae—II. Cytogeography of <i>Leavenworthia</i> .	
	<i>J. T. Baldwin, Jr.</i> 367
<i>Juniperus virginiana</i> , <i>J. horizontalis</i> , and <i>J. scopulorum</i> —IV. Hybrid	
Swarms of <i>J. virginiana</i> and <i>J. horizontalis</i> .....	<i>Norman C. Fassett</i> 379
On <i>Blakea</i> and <i>Topobea</i> .....	<i>H. A. Gleason</i> 385
<i>Ficus altissima</i> .....	<i>Mary F. Barrett</i> 394
The Ferns of Kashmir .....	<i>Ralph R. Stewart</i> 399
Index to American Botanical Literature .....	427
Inheritance of Orange and Yellow Flower Color in <i>Nemesia strumosa</i> .	
	<i>Herbert Parkes Riley</i> 435
The Variations and Origin of <i>Botrychium lanuginosum</i> .	
	<i>M. A. Chrysler</i> 454
The Discovery and Distribution of <i>Cinchona pitayensis</i> in Ecuador.	
	<i>William Campbell Steere</i> 464
Some Melastomaceae of Colombia .....	<i>H. A. Gleason</i> 472
<i>Juniperus virginiana</i> , <i>J. horizontalis</i> , and <i>J. scopulorum</i> —V. Taxo-	
nomic Treatment .....	<i>Norman C. Fassett</i> 480
Index to American Botanical Literature .....	483
The Shoot of <i>Botrychium</i> Interpreted as a Series of Dichotomies.	
	<i>M. A. Chrysler</i> 491
The Bryophytes of Shenandoah National Park, Virginia.	
	<i>Irma Schnooberger and Frances E. Wynn</i> 506
The Taxonomy of the Genus <i>Sauvagesia</i> (Ochnaceae) .....	<i>John D. Dwyer</i> 521
A New Section <i>Microphyllae</i> in <i>Agrostis</i> .....	<i>Alan A. Beetle</i> 541
Studies in the Sapotaceae—IV. The North American Species of <i>Manil-</i>	
<i>kara</i> .....	<i>Arthur Cronquist</i> 550
The Effect of Colchicine and Acenaphthene in Combination with X-	
Rays on Plant Tissue—I. Introduction .....	<i>Michael Levine</i> 563
Index to American Botanical Literature .....	575
Index to Volume 72 .....	587

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### ERRATA

- p. 341. In the first citation, for "*Phlyctochytrium Ameliae*" read "*Phlyctochytrium Aureliae*."
- p. 166. For [*Ceratostomella*] "*minutum*" read "*minuta*."
- p. 172. For [*Fomes*] "*ferruginosa*" read "*ferruginosus*."
- p. 177. For "*Sparassus*" read "*Sparassis*."
- p. 263. For [*Symphoricarpos*] "*leucocarpa*" read "*leucocarpus*."
- p. 404-406. Correct the varieties of *Nephrodium filix-mas* as follows: "*fibrillosa*" to "*fibrillosum*"; "*normalis*" to "*normale*"; "*Schimperiana*" to "*Schimperianum*."
- p. 409. For [*Polypodium*] "*africana*" and "*prolifera*" read "*africanum*" and "*proliferum*" respectively.
  - Change "*Gymnogramme*" to "*Gymnogramma*."
- p. 412. For [*Aspidium*] "*bakeriana*" read "*bakerianum*."
- For [Hook. Ic. pl.] "*17*" read "*1656*."
- p. 413. For [*Nephrodium aristatum* var.] "*affinis*" read "*affine*."
- p. 415. Change the varieties of *Asplenium filix-femina* and *Athyrium filix-femina* so that they end in *-um*.
  - p. 418. For [*Diplazium*] "*fraxinea*" read "*frazineum*."
  - p. 424. For [*Polypodium*] "*porosus*" read "*porosum*."
  - p. 426. For [*Polypodium*] "*brunnea*" read "*brunneum*."

## VACCINIUM HYBRIDS AND THE DEVELOPMENT OF NEW HORTICULTURAL MATERIAL

GEORGE M. DARROW AND W. H. CAMP<sup>1</sup>

There is every evidence that the indigenous Americans made considerable use of blueberries (*Vaccinium* spp.) as food (5, p. 585-588), and some Esquimo tribes to this day pick the fruit of *V. uliginosum* L., place it in skin bags and store these bags of blueberries in holes in the ground in contact with the permanently frozen zone. This apparently is a forerunner of our present out-of-season frozen "consumer package," a delicacy becoming more common on our own tables each year. The early settlers from Europe were not long in discovering this delectable addition to their fare. That the popularity of the blueberry is well deserved is indicated by the fact that, currently, a crop of a value ranging from \$5,000,000 to \$10,000,000 is harvested annually in the United States from wild, semi-wild, and cultivated plants. This is in addition to a widely cultivated member of the same group, the American cranberry [*Oxycoccus macrocarpus* (Ait.) Pers. (= *V. macrocarpon* of some authors)].

The blueberries are a polymorphic group of plants. Some species form large bushes (records of 20 feet high being common), while others under no circumstances exceed a stature of 15 inches. Some species produce few stems, some many stems from a common base, while others regularly form from small to extensive colonies by means of underground stolons. By using a leaf abnormality as indicator, one such colony has been traced and found to be at least a half-mile in diameter. From the standpoint of their horticultural development, other characteristics of importance are the marked differences between species in drought resistance, winter dormant period, size, flavor, and color of the fruit, keeping quality of the fruit (which is influenced by several anatomical features), the size and shape of the flowers, and the size of the seed. Apparently minor items may be exceedingly important; for example, because of the size and shape of the flowers not all blueberry corollas are equally accessible to the various species of wild and domestic bees whose visits are necessary for pollination and consequent fruit production. Such things must be taken into account in a breeding program.

Hybridization in our cooperative work on *Vaccinium* has a rather wide application. In the first place, it is the only means whereby the numerous divergent characters of the various species may be combined to produce the desired forms for further breeding and for the selection of new horticultural

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varieties. It is also an index of the ease with which interspecific hybrids may occur in nature and serves to explain many of the aberrant forms found in the wild. Moreover, it serves as a background for the study of the origin and nature of the various polyploid complexes found in the group.

#### HYBRIDS FROM CONTROLLED CROSSINGS

In this phase of the work the parent materials were brought into the experimental plots and greenhouses at Beltsville, Maryland, where the controlled crosses were made. The seedlings were grown in the greenhouse until ready to be set in the field test plots. Because the climate at Beltsville is not suitable for all species, especially those from the extreme South or North, extensive trial plots have been established at various places in New Jersey, Maryland, North Carolina, South Carolina, Georgia, and Louisiana, with smaller plots in other States.

To indicate something of the amount of material on which we have worked, in the years 1941, 1942, and 1943 approximately 18,000 plants from controlled crossings have been placed in the various test plots. The foregoing figure by no means represents the number of plants produced from controlled crossings—even during these 3 years. A complete genetic analysis of the material would necessitate that every effort be made to bring all members of a progeny to maturity for study. This, unfortunately, it has been impossible to do. In the first place, the nature of the project is such that rigid selection of the material must be practiced, even in the early stages of the plant's development and, therefore, individuals that did not meet certain horticultural standards were discarded almost immediately. Secondly, our facilities have limited the amount of material which could be handled, and plants have been discarded merely because of lack of space. However, efforts have been made to save as many types as possible as a basis for future work.

The following list, therefore, is merely an extract from the results of the work, indicating only the successful interspecific hybrid combinations produced under controlled conditions. To our own list have been added a few combinations previously reported by Coville (4) or known to have been made by him, the only change being that, in several instances, his nomenclature has been altered so as to coincide with ours.

#### Crosses between Diploids<sup>2</sup>

*V. tenellum* × *darrowi*

*V. pallidum* × *atrococcum*

*V. pallidum* × *myrtilloides*

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<sup>2</sup> Although there is disagreement among systematists on whether *Polycodium* should be treated as a separate genus or as a subgenus of *Vaccinium*, it is of considerable interest to note that Coville was able to produce viable hybrids between *Polycodium stamineum* (L.) Greene and *Vaccinium myrtilloides* Michx., both diploids. Since one parent is a deerberry and not a blueberry, this hybrid is omitted from this list. His records and specimens indicate that he also made a successful cross between *Polycodium melanocarpum* and *Vaccinium myrtilloides*.

### Crosses between Tetraploids

<i>V. corymbosum</i> × <i>virgatum</i>	<i>V. australe</i> × <i>virgatum</i>
<i>V. australe</i> × <i>simulatum</i>	<i>V. australe</i> × <i>lamareckii</i>
<i>V. australe</i> × <i>tallapusae</i> (= <i>alto-montanum</i> )	<i>V. australe</i> × <i>corymbosum</i>
<i>V. australe</i> × <i>myrsinites</i>	<i>V. australe</i> × <i>hirsutum</i>
<i>V. lamareckii</i> × <i>tallapusae</i> (= <i>alto-montanum</i> )	<i>V. australe</i> × <i>arctostaphylos</i> <sup>3</sup>
<i>V. lamareckii</i> × <i>virgatum</i>	<i>V. brittonii</i> × <i>myrsinites</i>
<i>V. lamareckii</i> × <i>hirsutum</i>	( <i>V. lamareckii</i> × <i>australe</i> ) × <i>virgatum</i>
<i>V. lamareckii</i> × <i>brittonii</i>	( <i>V. lamareckii</i> × <i>myrsinites</i> )
<i>V. lamareckii</i> × <i>myrsinites</i>	× <i>australe</i>
	( <i>V. lamareckii</i> × <i>australe</i> )
	× <i>myrsinites</i>

### Crosses between Hexaploids

<i>V. ashei</i> × <i>amoenum</i>	<i>V. ashei</i> × <i>constablaei</i>
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### Heteroploid Crosses

<i>V. angustifolium</i> (2x) × <i>tallapusae</i> (4x) (= <i>alto-montanum</i> )	<i>V. australe</i> (4x) × <i>ashei</i> (6x)
<i>V. australe</i> (4x) × <i>amoenum</i> (6x)	<i>V. australe</i> (4x) × <i>constablaei</i> (6x)
	<i>V. simulatum</i> (4x) × <i>ashei</i> (6x)

There is also on hand a fairly large amount of cleaned and prepared seed from the 1942 and 1943 crosses. It is our experience that plump seed generally indicates the presence of viable embryos and successful germination though not necessarily fertile hybrid plants. The following list, therefore, indicates possible additional successful interspecific combinations.

### Seed Obtained from Diploid Crosses

<i>V. myrtilloides</i> × <i>tenellum</i> (seed germinated)	germinated)
<i>V. myrtilloides</i> × <i>pallidum</i>	<i>V. darrowi</i> × <i>pallidum</i> (seed germinated)
<i>V. myrtilloides</i> × <i>elliottii</i>	<i>V. darrowi</i> × <i>ovatum</i> <sup>4</sup> (seed germinated)
<i>V. darrowi</i> × <i>elliottii</i> (seed	

### Seed Obtained from Tetraploid Crosses

<i>V. lamareckii</i> × <i>arkansanum</i>	<i>V. myrsinites</i> × <i>arkansanum</i>
<i>V. tallapusae</i> (= <i>alto-montanum</i> ) × <i>virgatum</i> (seed germinated)	

### Seed Obtained from Heteroploid Crosses

<i>V. darrowi</i> (2x) × <i>australe</i> (4x) <sup>5</sup>
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<sup>3</sup> Of considerable interest because *V. arctostaphylos*—a species native in the Caucasus of Asia Minor—is generally placed in a section of the genus quite apart from *V. australe*.

<sup>4</sup> *V. ovatum* is an evergreen species of the West Coast of North America; *V. darrowi* is also evergreen. No plants have resulted from previous crosses involving *V. ovatum* with other species.

<sup>5</sup> We await the mature plants of this cross, as well as of *V. angustifolium* × *tallapusae* (= *alto-montanum*) of which we have a few plants, with considerable interest so that morphological and cytological examinations may be made. Pentaploids are produced with ease and have been found in the wild. Thus far, triploid plants are unknown. It is to be noted that this particular diploid × tetraploid cross yielded only about 20 seed, whereas the tetraploid × hexaploid combinations were generally much more successful, in one instance (*V. virgatum* × *ashei*) yielding a harvest of approximately 5,000 seed.



<i>V. tallapusae</i> (4x) × <i>ashei</i> (6x)	<i>V. lamarckii</i> (4x) × <i>ashei</i> (6x)
<i>V. australe</i> (4x) × <i>constablaei</i> (6x)	<i>V. myrsinites</i> (4x) × <i>ashei</i> (6x)
<i>V. virgatum</i> (4x) × <i>ashei</i> (6x)	<i>V. myrsinites</i> (4x) × <i>constablaei</i> (6x)
[ <i>V. australe</i> (4x) × <i>ashei</i> (6x)] (5x) × <i>ashei</i> (6x)	
[ <i>V. australe</i> (4x) × <i>ashei</i> (6x)] (5x) × <i>australe</i> (4x)	

#### HYBRIDS OBSERVED IN THE WILD

It is not always safe to assume that plants exhibiting the characters of two other species are hybrids; they may be part of a highly segregative allopolyploid population. This has been discussed elsewhere in a consideration of the genetic structure of the allopolyploid species (3, p. 342-346, 363, 364). Yet those who are reasonably familiar with the material, and are aware of the pitfalls, may often distinguish between hybrids and allopolyploid populations with some degree of accuracy. In our joint field work we have repeatedly noted individuals and communities which apparently were of hybrid and segregate origin, possessing characters of two species which, in that region, made distributional contact. Some of these hybrid combinations will be noted here, with a brief discussion of each. It should not be assumed that many of the hybrid plants are  $F_1$ . In fact, they are back-cross and segregate plants of diverse inheritance.

#### Diploid Hybrids

*V. ELLIOTTH* × *DARROWI*. The mayberry, *V. elliotii*, is somewhat variable, one of its phases (for example) having leaves that are reduced in area, relatively narrower, and more indurated than is typical; they are also inclined to be tardily deciduous. The observed hybrids indicate that this combination is very likely to have been the source of such aberrancies, since *V. darrowi* is small- and narrow-leaved, and evergreen. Nearly intermediate plants (possibly  $F_1$ ) are essentially evergreen.

*V. ELLIOTTH* × *ATROCOCUM*. Typically *V. elliotii* is glabrous; where its leaves are more or less pubescent, this pubescence, to a considerable extent, seems to have come from *V. atrococum*. In the same areas where this variation occurs, the characters of *V. atrococum* also are often blurred, the plants becoming more like *V. elliotii*.

*V. TENELLUM* × *DARROWI*. Apparently locally common. *V. tenellum* is glandular and deciduous, whereas *V. darrowi* is eglandular and evergreen. When experimentally produced from material typical of each species, some  $F_1$  plants are glandular and completely evergreen and in these (and other) characters scarcely to be distinguished from the well-known *V. myrsinites*, a segregative tetraploid. If plants taken casually from the wild are used as parental material, the resulting progeny may vary toward one or the other parental type, indicating that these species—as taxonomic units—are not genetically pure.

*V. TENELLUM* × *PALLIDUM* and *V. TENELLUM* × *VACILLANS*. As will be noted in a later paper of this series, there are areas where *V. pallidum* and *V. vacillans* have hybridized, producing more or less blended populations. However, in certain areas in the Southeast, on the outer Piedmont and on the boundary between the Piedmont and Coastal Plain, material apparently rather typical of *V. pallidum* may be found. Where present in the same areas with *V. tenellum*, the two hybridize. Plants more closely related to *V. vacillans* are also present in this same general region; these too hybridize freely with *V. tenellum*. From the appearances of the wild populations, and the evidences of gene-exchanges, it would seem that these species are particularly adapted to genetic studies.

*V. ATROCOCIMUM* × *DARROWI*. It is seldom that these two species appear in the same habitat; yet, where they do, most unusual series of plants result. One such community was found to run the gamut of variation between these two widely contrasting species—that is, highbush to lowbush, few stemmed to extensive colonies, macrophyllous to microphyllous, pubescent to glabrous, deciduous to evergreen, etc.

*V. ATROCOCIMUM* × *VACILLANS*. An exceedingly common combination, producing—by segregation and genic infiltration—highly polymorphic populations, one of which has been described in some detail in another place (3, pp. 360–362). Wild plants have now been examined and prove to be diploid. Segregates of this combination have been described as *V. vacillans* var. *crinitum* Fernald. Populations described as *V. margarettae* Ashe and *V. missouriense* Ashe also seem likely to prove to be segregates from this combination.

*V. ATROCOCIMUM* × *CAESARIENSE*. This combination is relatively common in certain areas along the eastern Coastal Plain, and the populations of both species give evidence of having exchanged genes.

*V. TENELLUM* × *ELLIOTTII*. Where these two come together, numerous colonies have been found that exhibit a variety of segregate characters derived from both species. Plants from the wild have been found to be diploid. Material much like this was the basis of *Cyanococcus cuthbertii* Small [= *Vaccinium cuthbertii* (Small) Uphof]. The type sheet is a mixed collection, but appears to be this combination (see next paragraph).

*V. TENELLUM* × *CAESARIENSE*. A considerable number of plants, probably of this combination, are known. A series of herbarium specimens was included by Small in *Cyanococcus cuthbertii*; it seems to have contained material of this and of the preceding combination, its polymorphic nature being held together—in definition—on the basis of the characters derived from the common ancestor, as well as the circumstance that both of the other ancestral species are highbush. The *V. tenellum* × *elliottii* combinations are easily separated from those of *V. tenellum* × *caesariense* if one looks for the sur-

viving characters in the combinations which serve to distinguish *V. elliottii* from *V. caesariense*.

*V. CAESARIENSE* × *DARROWI*. Evergreen plants, 1–2 meters high, have been found in northern Florida that would seem to be this combination. Several that have been examined have proved to be diploid.

*V. ANGUSTIFOLIUM* × *MYRTILLOIDES*. Apparently rare; but the increase of pubescence in *V. angustifolium* in areas where these species make contact, together with a partially serrulate condition in the otherwise entire leaf of *V. myrtilloides* (coupled with a loss of some pubescence), leads to the conclusion that natural hybrids do occur.

*V. ANGUSTIFOLIUM* × *VACILLANS*. Reciprocal morphological disturbances are to be noted where they make distributional contact. These disturbances are considerably more pronounced in *V. vacillans* than in *V. angustifolium*. Today, *V. vacillans* is invading the southern part of the range of *V. angustifolium*, in which this latter species is generally represented only by residual (and often ancient) clones which, of course, exhibit no evidence of the part they have played in the production of sometimes confusing plants. *V. dobbini* Burnham appears to have been described from plants of this combination; derived allotetraploids may also be present.

*V. MYRTILLOIDES* × *ATROCOCUM*. The northern margin of the range of *V. atrococum* slightly overlaps the southern margin of the range of *V. myrtilloides*. Being more or less confined to boggy areas in these two extremes of range, they make contact in certain localities. Where this happens, plants clearly intermediate in character may be found.

*V. ANGUSTIFOLIUM* × *CAESARIENSE* and *V. ANGUSTIFOLIUM* × *ATROCOCUM*. “Halfhigh” plants, presumably of these combinations, have been found with the parents. Too often, however, the analysis is complicated by the presence of the tetraploids *V. corymbosum* and *V. lamarckii* in the same habitat; these also yield halfhigh plants with very similar characters, as will be noted in a later paragraph.

### Tetraploid Hybrids

*V. MARIANUM* × *AUSTRALE*. Along the eastern Coastal Plain south of the glacial boundary, areas may be found where *V. marianum* occurs with *V. australe*; there the usual homogeneity of *V. australe* is disturbed, and it is concluded that this is the result of gene-exchange with *V. marianum*. This whole situation will be taken up in more detail in a later paper of this series.

*V. BRITTONII* × *LAMARCKII*. Although morphologically quite similar and long confused in herbaria, *V. brittonii* has glaucous leaves and twigs, and black fruit, whereas *V. lamarckii* has bright green, nonglaucous leaves and twigs, and glaucous fruit. Where these two chance to meet, plants are found that have reciprocal segregate characters. The two species hybridize easily under controlled conditions.

**V. CORYMBOSUM.** Our analysis of the polymorphic, tetraploid highbush population north of the glacial boundary—treated as *V. corymbosum* in manuals—leads us to the conclusion that it represents nothing more than an enormous collection of interbreeding hybrid segregates which had its origin in the Pleistocene. For the most part, it seems to have been derived from the tetraploids *V. australe*, *V. marianum*, *V. simulatum*, and *V. arkansanum*, which are to be found in reasonably pure form, today, only south of the glacial boundary. This matter has been discussed by Camp (2, p. 201, 202) and by Camp and Gilly (3, p. 347, 348, under the mictonic species); it will be expanded more fully in a later paper.

**V. BRITTONII**  $\times$  **CORYMBOSUM** and **V. LAMARCKII**  $\times$  **CORYMBOSUM.** The tetraploids *V. brittonii* and *V. lamarckii* (both lowbush) are likely to occur in conjunction with the highbush *V. corymbosum* in areas which have been ecologically disturbed. Where they are found together, plants more or less intermediate in stature and possessing all manner of segregate characters are to be found. The halfhigh bushes are so common that they are found in large numbers in certain herbaria. It is primarily by means of these two lowbush entities that the already inherent polymorphy of *V. corymbosum* has been considerably enriched. It is most difficult, if not impossible, to distinguish with certainty between the foregoing tetraploids and the diploid segregates of *V. angustifolium*  $\times$  *atrococcum* and *V. angustifolium*  $\times$  *caesariense* on the basis of herbarium material, and quite as difficult in the field where both diploids and tetraploids are present in the same locality.

**V. ALTO-MONTANUM**  $\times$  **SIMULATUM.** As will be noted in a later paper dealing with the taxonomy of the blueberries, *V. alto-montanum* appears to be made up of several biotypes, one of which was described as *V. tallapusae*. Both the high-mountain type (the original *V. alto-montanum*) and the form from lower elevations (*V. tallapusae*) appear to hybridize with *V. simulatum* where their ranges meet.

**V. SIMULATUM**  $\times$  **ALTO-MONTANUM**  $\times$  **LAMARCKII.** A series of specimens from near Mountain Lake, Giles County, Va., indicates that *V. lamarckii* is still present this far south. In the same region plants of the apparently tetraploid *V. alto-montanum* may also be found, as well as the known tetraploid *V. simulatum*. While the typical material of all 3 tetraploids for the most part is reasonably ecologically disjunct in the second-growth forest (where sufficiently open) and around meadows and abandoned fields, plants are present that exhibit characters derived from the various paired combinations, with some individuals apparently involving all three species.

**V. MYRSINITES**  $\times$  **AUSTRALE.** Controlled crosses match material found in the wild, the only difference being the greater variability of the wild populations. This is obviously the result of sufficient time in the wild for the production of segregate and back-cross individuals.

"SOUTHERN HYBRID COMPLEX." Five species, all apparently tetraploid, namely, *V. virgatum*, *V. myrsinites*, *V. fuscatum*, *V. australe*, and *V. arkan-sanum*, are to be found growing together in various combinations in parts of the Coastal Plain region of South Carolina, Georgia, Florida, and Alabama. Where two or more of these come together they form hybrids in all possible combinations, at times yielding local populations which, taxonomically, are almost unsolvable. Unlike the northern tetraploid complex (*V. corymbosum*), which appears not to have produced any hexaploids, the southern tetraploid hybrid complex has been the source of numerous and polymorphic populations of hexaploids, to which the name *V. ashei* is here collectively applied.

### Hexaploid Hybrids

*V. AMOENUM*  $\times$  *ASHEI*. There are strong indications that, phyletically, *V. amoenum* is not one of the segments of the *V. ashei* complex, although hexaploid plants derived out of *V. virgatum*  $\times$  *australe* combinations would be likely to yield segregative extremes superficially similar to it. Instead, it appears to be the culmination of a *V. tenellum* (2x)—*virgatum* (4x)—*amoenum* (6x) autopolyploid series, in which pentaploids also are known from the wild. However, the distribution of *V. amoenum* is such that it touches various segments of the *V. ashei* complex. Where this occurs, hybrids, segregates, and back-crosses are to be found, thus adding to the nomenclatural difficulties of an already perplexing situation.

### POSSIBLE REASONS FOR THE ABUNDANCE OF NATURAL HYBRIDS

The question has been raised: "If homoploid blueberries hybridize so easily, why is it that, long ago, they did not become more thoroughly mixed at the different levels of chromosome numbers, resulting in the development of three large amalgamated populations, namely, diploid, tetraploid, and hexaploid?" It must be admitted that there are areas where this would seem to be the easiest solution of our taxonomic problems. But, in answer to that question, we might say that our field studies indicate that conditions for such mixing were by no means common before the advent of the white settlers. Where we have pursued our studies in relatively undisturbed areas, it is indeed rare to find different homoploids occupying the same habitat. That is, there were factors of geo-history and physiology which favored the development and maintenance of geographically and ecologically disjunct homoploids. It has been the disturbance of the ecological balance—the extensive and repeated clearing and burning, the formation of fields and pastures, and often their later abandonment—which made it possible for the various homoploid blueberries to enlarge their ranges and thus make contact, especially since they are a favorite food-source for birds and thus are easily distributed. Because these disturbances favor its dispersal and enlargement of

range, the blueberry population of eastern North America today probably contains enormously more individual plants than it did at the advent of the white settlers; and it is likely that as many interspecific hybrid blueberries have been naturally produced in the last hundred years as in the preceding ten thousand years.<sup>6</sup>

In analyzing the situation, it is our observation that bees are the chief agents of pollination in *Vaccinium*. It has also been noted by many that during the height of the flowering season, individual bees may be selective, visiting only certain species. However, since blueberries flower at the beginning of the vernal period when other nectar-bearing species are at a premium, bees are very likely to be much less particular. We have paid some attention to this item on various occasions and have watched individual bees visit several species of *Vaccinium* in succession; in fact, a scarcity of available flowers only adds to the chance of producing hybrids, for, if two species have somewhat different blooming periods, the latest flowers of one species are likely to be open at the same time as the earliest flowers of the other. Thus the way is opened for the production of interspecific hybrids.

Another item should be noted. We have long observed that isolated colonies of some species are likely to be much less fruitful than those found in the vicinity of another homoploid species. It would seem to follow from this that many individual plants of *Vaccinium* are essentially self-sterile. This, however, is not entirely true; the controlled breeding work so far carried out by ourselves, Morrow (8), and others would seem to indicate the following:

1. While individual plants may be essentially self-sterile, others of the same species may be partially, or even considerably, self-fertile.
2. Those most nearly homozygous are more likely to approach self-sterility than heterozygous individuals.
3. It seems to be usual that individuals even of highly divergent homoploid species are more capable of producing good sets of fruit and more vigorous seedlings when hybridized than when these same individuals are selfed.

In the blueberry there seems to be no interspecific sterility between homoploids. Each species seems to have a basic genom set which is compatible with that in other species. Because self-sterility occurs to a greater or lesser extent in the genus, the development of species seems to have been determined more by geographical and ecological isolation than by genetical isolation.

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<sup>6</sup> However, we must not forget that certain natural populations (e.g., *V. corymbosum*), which today are widespread, are the result of mass hybridizations during and after the Pleistocene, the result of readjustments along the distributional margins of several homoploids, following large scale climatic and ecological disturbances.

Another item leading to the production of large wild populations of hybrid blueberries is the fact that birds are the primary vectors of the seed. Since the individual fruit commonly contains 10–70 seeds, it is more than likely that the majority of those from a single crossing will be passed at the same time and thus eventually form the nucleus of an interbreeding population. And even if the seed were to be scattered somewhat by subsequent rains or otherwise, it would be that much better, for with competition thus reduced, a larger percentage would be likely to survive; in any event, it is unlikely that the majority would be carried so far that they would not be considered as part of the same potential breeding community. Thus, in spite of the fact that considerable self-sterility exists in *Vaccinium*, the chance of survival and spread of hybrid and segregate populations is notably increased by the manner in which the seed is distributed.

In addition, we must not ignore the fact that the individuals of most species of *Vaccinium* are long-lived perennials. If, for instance, we consider the colony with distinctive leaves alluded to in our opening remarks, and which apparently was not less than a half-mile in diameter, we may roughly calculate its age. This particular clone (belonging to the *V. myrsinites* complex) put out annual underground stolons which seemed to average about a foot in length. If we assume that this clone radiated from its exact center—and that its rate of peripheral growth has been constant—it may be calculated that this plant is not less than 1,000 years old. It may be much older. Nor would this seem to be exceptional, for there is considerable evidence that certain clones of the distantly related box huckleberry (*Gaylussacia brachycera*) have persisted for untold thousands of years, at least since the late Pliocene, or early Pleistocene (1).

Thus, even if an individual did exist which was self-sterile—and near which no other homoploid plants existed—there would be no concern over its immediate fate. If the habitat were congenial, it could persist for at least several milleniums, during which time some adventurous or wind-blown bee might bring a supply of pollen from a homoploid plant, or a passing bird might pause in its branches for a moment and deposit a few seeds of a homoploid plant, thereby setting the stage for another hybrid population. Time and chance must be reckoned with in our considerations.

This longevity of individual clones plays another important role in the production of interspecific hybrids. Following long-term climatic cycles, or more rapidly effective ecological disturbances caused by man's activities, the habitat or ecological association may be so changed in a given area that the general population of one species will be replaced by that of another, better able to persist under the new conditions. However, it is likely that there will always be a few micro-habitats where individual plants of the retreating species will persist long after they have been surrounded by the

advancing species. In line with the foregoing generalities, several specific examples will be mentioned.

There is every evidence that the main body of the population of the diploid *V. angustifolium* has been migrating northward since the last of the Pleistocene glaciations, a movement no doubt accelerated by the post-Pleistocene xeric period. Where once obviously common, it is today known in the highlands south of its present center of abundance in restricted areas, generally in isolated colonies. As the climate shifted and new ecological associates came in, its former sites were taken over by the diploids of the *V. vacillans* complex, better adapted to higher temperatures and dryland conditions. Actually, several of these remaining southern stations of *V. angustifolium* have been located by noting the direction of increase in the proportion of *angustifolium*-like characters in the invading population, the more obvious of which are the decrease in plant and leaf size, and change in leaf shape, coupled with increases in the amount of leaf serration and general "twiggy" condition. In other instances the pure *V. angustifolium* has not been found, but its characters are evident in the plants which have taken over the sites where it must have lingered longest, and where it could have hybridized with the invading plants when they first entered the area.

Other examples are the direct result of man's activities. When observed under undisturbed conditions, the individuals of the northern highbush species are to be found usually in the shrub zone surrounding lakes and open bogs; back of this is a zone of lowland forest with shade so dense as to exclude species of *Vaccinium*. The uplands, having a more open forest type and often with rocky exposures, support populations of various lowbush species. This, therefore, must have been the situation at the advent of the white settlers, for the indigenous Americans, as a general thing, did not carry on an extensive agriculture. Following the clearing of both forest types, the settlers often made attempts to keep these areas open and available for pasture by means of repeated fires. Such conditions exclude the highbush species, but are no bar to the lowbush species because of their underground stolons. Indeed, occasional burning makes these forms more productive. Thus, the lowbush forms, once confined to the uplands, could now successfully migrate into the lowlands sufficiently close to make genetic contact with any homoploid highbush material present. Specific examples which might be cited are the tetraploid combinations of *V. brittonii* and *V. lamarckii* with *V. corymbosum*, and the combinations of the diploids *V. atrococcum* and *V. vacillans*. The same process to a large extent has also been exceedingly active around the pond and slough margins in the southern and southeastern Coastal Plain, other species, of course, being involved.

Since clearing activities produce drier and more sunny habitats, and in the lowlands are often followed by attempts at draining, other effects may



sometimes be noted following the formation of such hybrid communities. In our studies, we have found certain areas where hybrid populations have persisted after the parents have become extinct in the locality. One such instance has been noted in eastern Louisiana where combinations of the highly divergent *V. elliotii* and *V. darrowi* are involved. In fact, such hybrid populations may be particularly suited to some environment and so able to migrate into areas which exclude the parents. For example: certain valleys in Georgia and Alabama, which are pastured and occasionally burned over, have abundant stands of a combination between *V. elliotii* and *V. tenellum*. Here, the rank pasture grass excludes the low-growing *V. tenellum*, and the fire excludes the highbush *V. elliotii*; whereas, the *V. elliotii*  $\times$  *tenellum* combinations are successful because they are clone-forming and persist by means of underground rhizomes which are not injured by the fire, and yet the plants are sufficiently robust and high-growing to compete with the grass. These populations, in many instances, seem to have migrated down the valleys from the upper reaches and headwaters where *V. tenellum* and *V. elliotii* come together, and where the basic members of the hybrid population were produced. It was probably just such a population migrating down a valley in Georgia that led to a recognition of the material first described as *Cyanococcus cuthbertii* (see the previous discussion of *V. tenellum*  $\times$  *elliotii* in this paper).

One of the writers of this paper has been observing a highly polymorphic local population of the *V. corymbosum* complex in northeastern Ohio over a period of 25 years—or even longer, if one were to include those times when, as a lad, he ventured into it in quest of berries. During this time the area has been selectively cleared, partly drained, and later intermittently pastured. There was at first a considerable reduction in the total number of plants, and the general aspect of the population has since become markedly changed through natural selection. The remaining segregate biotypes are now becoming effectively established and, barring some new ecological disturbance, seem well on the way toward recapturing most of the available area.<sup>7</sup>

From the foregoing, it may appear that we have placed undue emphasis on our study of natural hybrids. Yet, they are so ever-present that they cannot be ignored, or even dismissed with a brief discussion. Frankly, it was this study of uncontrolled hybrid populations in the wild which opened to us the tremendous possibilities for the horticultural development of the

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<sup>7</sup> During one stage of this investigation, a large series of the plants was marked with metal tags, so that particular individuals could be revisited and observed at various seasons and over a period of years. Although the data obtained from the study of this population have never been presented in one place, the numerous and involved questions which arose have had considerable to do with directing the lines into which the present studies of the genus *Vaccinium* have developed.

genus. In fact, in our work we have come upon certain areas which are little else than glorified field laboratories and experimental plots, their populations so diverse that a lifetime of concentrated effort would scarcely begin to duplicate their complexity. In such areas, our work has consisted of the selection of those individuals most likely to be of horticultural value, as well as an attempt to determine the basic species and genetic processes involved. It is scarcely necessary to note that a full understanding of the methods whereby such populations develop is necessary before the taxonomy of the genus can become stabilized.

Furthermore, although we were not aware of it in the beginning, our studies of hybrids have given us the key to a further understanding of the nature and origin of the even more complex allopolyploid populations, so characteristic of the genus. It must have been out of just such hybrid populations that the allopolyploids of the past arose; today, to our certain knowledge, it is where the newer ones are being produced. Taxonomically, these hybrid complexes and allopolyploid complexes are provocative; horticulturally, they are rich in new and worthy combinations.

#### THE DEVELOPMENT OF NEW HORTICULTURAL MATERIAL

In the development of new and better horticultural material in blueberries, numerous factors are involved. By their very nature, there is not, and probably never will be, such a thing as an all-purpose variety. Let us, for example, consider a single item—the fruit.

Among the fruit qualities to be considered are flavor, size, texture, and color. Yet, having achieved an apparently desirable combination of these characters, other factors must be considered. Are the berries to be used as fresh fruit, are they to be “quick frozen,” are they to be incorporated in rapidly-baked pastries, or are they to be canned, and if canned, is their ultimate destiny to be a conserve, a dessert, or an ingredient of pastries? Now this may seem needlessly detailed and considerably involved, but the fact remains that there is a remarkable difference in the reactions of the various kinds of blueberries to the factors of transportation, storage, and the various types of processing and cookery mentioned above.<sup>8</sup> Even the vitamin C content and its stability in storage is known to vary considerably among varieties (6). In general, therefore, the breeder does not attempt the production of an all-purpose berry; instead, a series of special types must be achieved, adequate for the various needs of the trade as well as the home garden.

It should be noted here that the so-called different “brands” of blueberries put on the market by several of the larger Eastern growers’ associa-

<sup>8</sup> For example, considerable differences have been noted between various varieties in their reactions to freezing in “consumer packages” (7).

tions refer to no horticultural variety; they represent merely size-classes of the berry. Of course, the growers recognize marked differences in the quality of the varieties under cultivation, but as yet they have made no extensive attempt to educate the buying public. But the day would seem to be not far distant when the careful housewife, the discerning restaurateur, and the progressive packer or canner will demand certain varieties, just as they do of apples, pears, or peaches.

So far as flavor is concerned, in blueberries (as in many fruits) it apparently is the result of a balance between sugars, organic acids, and one or more aromatic compounds, these last generally being present in minute quantities. It is these aromatic compounds that are responsible for the characteristic "blueberry flavor." Some clones produce an overabundance of aromatics; as a result the fruit has a pronounced musky flavor. Fortunately, the aromatics are subject to genetic control and can be built up or attenuated as needed. The same may be said of the sugar and acid content of the various types. In general a so-called "sweet" berry is not necessarily one that has an abundance of sugar but rather one with a relatively low acid content. Of course, climatic factors also affect flavor. It has been noted in many varieties that sunny days and cool nights tend to develop the highest flavor. But, even so, there is a fundamental genetic difference between varieties in their ability to respond to favorable conditions of light and temperature. Flavor, therefore, is within the control of the breeder.

Size of berry is somewhat unpredictable. In general, the higher polyploids of a series have larger fruit than the species with fewer chromosomes. So far, selection and cross-breeding of the larger-fruited sorts seems to have given the best results. Unfortunately for the industry, some of the larger-fruited commercial varieties achieved their prominence largely on the basis of size. For example, the Cabot (fig. 1) was one of the first varieties introduced and in general it has poor dessert quality. From this arose the false supposition that "big berries are not good-flavored." In contrast, Stanley, Pioneer, and other varieties now in cultivation refute this idea. Even the Dixi with berries almost an inch in diameter has better flavor than most wild blueberries. As yet we have no idea what the upper limit of the size of the berry will be (fig. 2). To date, 2 selections have produced fruit in excess of an inch in diameter. However, there might be drawbacks to fruit of such size. In the first place the main axis of the fruit cluster ordinarily is not large enough to support this size of berry, resulting in crowding to the extent that the fruit either is angled, or is forced off the pedicels before the pickers arrive. Since the finding of the Rubel with unusually long internodes on the main axis between the individual pedicels as well as with long pedicels, large-fruited varieties have been bred that do not crowd in the cluster, such as Atlantic, Pemberton, and Jersey. Also, for many purposes a fruit much in excess of an inch in diameter would seem to be undesirable.

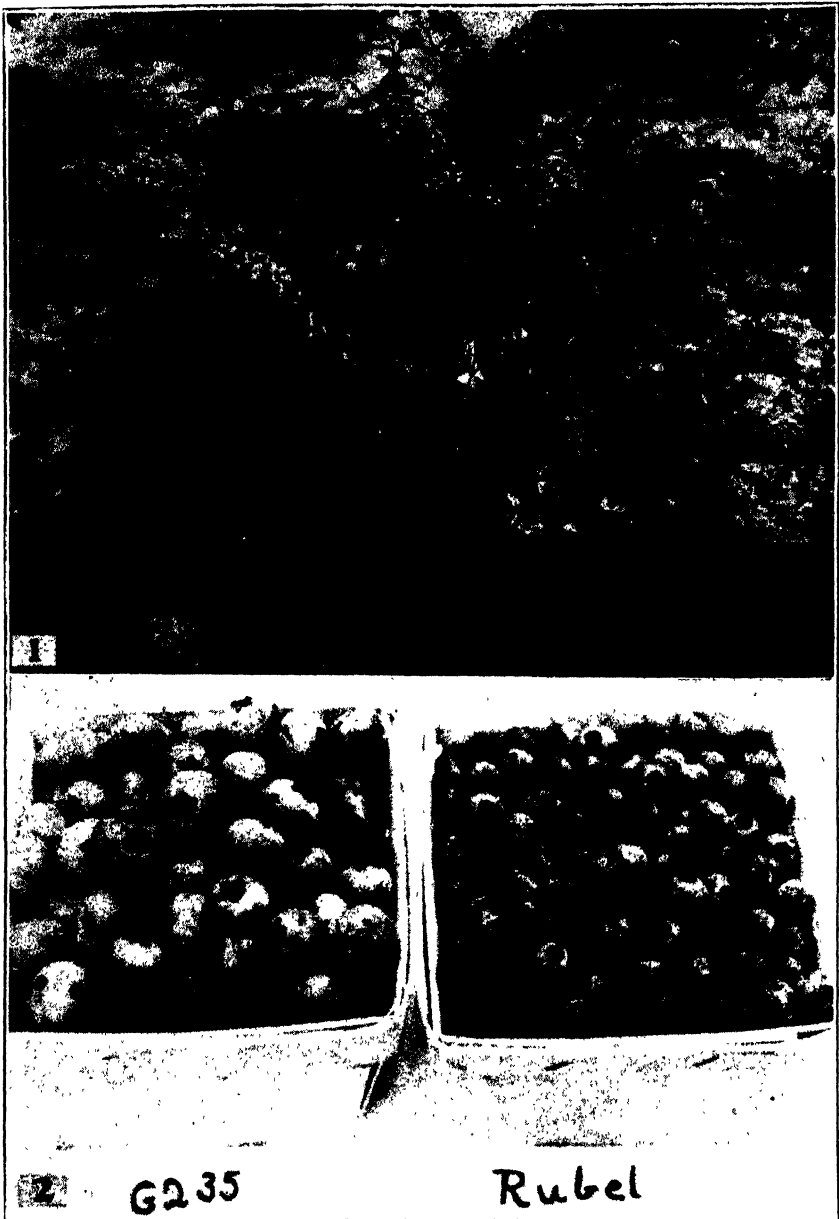


FIG. 1. A plant of the Cabot variety about 3 years old. FIG. 2. Right, fruit of the Rubel variety, the best selection yet taken from the wild; left, a large-fruited selection, the result of breeding work. Photographs from the U. S. Department of Agriculture.

Texture has been a rather elusive quality, but is now becoming understood. Several species are known whose fruit with ordinary cooking is unappetizing. They owe this undesirable quality to the presence of large seed and hard placental tissue. However, our field studies indicate that several of the "pulpy" and "seedy" species of berries easily make genetic combinations in which a balance is achieved, the hybrids producing fruit with crisp flesh of high dessert quality. Following this lead, thousands of plants have been produced within the last few years by controlled matings between selected parents of both types. The possibilities of firm-textured berries of good quality, and their advantages to the canning industry and to those growers who must ship long distances are obvious.

The actual color of most fully ripe blueberries is a deep purple-black, but in many species this is masked by a glaucous covering which gives the fruit its characteristic bluish color and is responsible for the common name of the plant. Actually, this covering is an oil-air emulsion which becomes waxy and, as such, is easily lost in handling. Since it is traditional that the blueberry should be "blue" it is of considerable commercial importance that this covering be retained until the fruit is marketed. Unfortunately, some of the better-flavored wild species, and a few of our selections of others, have little or none of this covering and, therefore, are of low commercial value; even berries from cultivated plantations often reach the consumer in poor condition so far as the appearance of the package is concerned. Conversely, we now have available selections from the wild which have a very heavy and durable coating; because of this, they have been called "aluminum berries." These individuals have been found in several species [e.g., *V. myrtilloides* (2x); *V. lamareckii* and *V. alto-montanum* (4x); and *V. constablaei* (6x)].

Another fruit character which should be mentioned is keeping quality. Other things being equal, the deciding factor in the keeping quality of the fruit is the type of scar produced in picking when the berry is separated from the pedicel. If the "brush" (the ends of vascular bundles) separates cleanly leaving a small, smooth, shallow hole with no exudate of sap, the berry ordinarily keeps well; but if some of the epidermis and flesh is torn and removed with the pedicel, organisms of decay soon gain entrance and ruin the fruit. Even if such berries do not decay they shrink badly by drying. Although several of our best-flavored species (tetraploids as well as hexaploids) typically have very bad scars, this may be corrected by selection of plants having fruits with good scars and through controlled crossings with homoploids having nearly perfect scars [e.g., certain selections of *V. lamareckii* (4x), *V. virgatum* (4x), *V. alto-montanum* (4x), and *V. ashei* (6x)].

The length of the period of bud dormancy is important. For example: the commercially most important northern species require a winter dormant

period of at least 800 hours below 45° F, whereas the Gulf Coast species, *V. ashei*, breaks dormancy after less than 250 hours and *V. myrsinites* with a much shorter exposure to this temperature. When such species are used in breeding, care must be taken that the selections for use in particular latitudes have the correct dormant-period requirement, otherwise they may either not break dormancy, or push out too soon and so be injured by late frosts.

From the commercial standpoint, the date of ripening is of great importance. The determining factors are the date of flowering and the length of time required for the ripening of the fruit. Individual clones in the test plots show considerable differences in both these factors; thus, through the use of different horticultural varieties whose habits are known, the grower can markedly extend the season for fresh fruit.

Another characteristic is the length of time over which fruit continues to ripen on the plants. Obviously, it is to the advantage of the commercial grower to have the picking season for a given variety concentrated in a relatively short period, for the reason that production costs are prohibitively increased when the pickers are forced to return repeatedly to the same plants, each time getting only a small portion of the crop. For example, this is one of the faults of the southern "rabbiteye blueberries" (*V. ashei*), in which the picking season is spread over a period of 30 or more days and in some instances of 90 days. Such a length of season is an advantage for the home grower but a disadvantage for the commercial grower. It is considered a serious fault also of the Cabot highbush variety, which has a picking season as long as 40 days. Here two factors are involved; one is the extreme length of the flowering period in the individual inflorescence; and the other is the irregularity in the breaking of dormancy of the inflorescence buds. Careful selection of the better wild clones, together with controlled crossings with other homoploids which do not have this fault, should yield material with considerably improved flowering habits.

Other plant characteristics must also be considered. Here there is a wide range of variables from which to choose; fortunately, plant habit is genetically controlled. From the standpoint of the grower, a plant should produce shoots freely, but not too freely. There should always be on hand a sufficient supply of young, vigorous canes, but they should not be produced in such abundance that the individual plant gets out of hand, interfering both with cultural practices and production. Some of the material is essentially single stemmed and therefore not acceptable for field plantings; other selections tend to sucker excessively and thus produce unwieldy plants. But with these widely contrasting types now available for breeding, it is possible to breed and select varieties of any growth habit desired.

The foregoing has a direct bearing on one of the more important cultural practices in commercial plantings, that of pruning. The majority of high-

bush commercial species each year put forth from the base of the plant several to many new shoots which normally rise to a height predictable for that particular variety. These shoots may grow to full height in one season though usually not until after two or three seasons. These stems or canes may bear when one year old in the case of lowbush species or not until after two or three years in the case of the highbush species. For several successive seasons the plants bear heavily from short (and generally subterminal) branchlets called laterals. After the first year with the lowbush and after several years with the highbush there is a notable decline in the abundance of the crop and the size of the berries, making it advisable to remove the old wood so that a continuous succession of vigorous shoots is available. For this reason lowbush fields are burned over and highbush fields are pruned. Since height is under genetic control and there is available material from 15 inches to 15 feet high, a plant of any desired height between these extremes can be obtained. Lowbush selections with stouter stems and highbush selections of greatest vigor may prove to be the most desirable types.

It has long been supposed by many that commercial blueberries must be grown in areas with sandy soil, a permanently high water table, and with no extreme summer temperature. It may therefore surprise some to learn that, even today, nearly one-half (2,000 to 3,000 acres) of the commercial plantations of highbush blueberries in the United States are of *V. ashei*, and that these are located in Florida (and to a lesser extent in southernmost Alabama and Georgia) generally on upland, often clayey, soils subject to severe drought, where the plants are exposed to high summer temperatures. Nor is there any way to arrive at more than a rough estimate of the size of the crop picked annually from the wild plants of *V. tallapusae* (= *alto-montanum*) and *V. pallidum* in the dry hill-region of Georgia and Alabama. And if one wishes to visit an area which, at times, can be excessively dry and hot, one has only to follow down the Florida peninsula, the natural range of *V. myrsinites*. These are only a few of the species that are not found in wet places and that thrive under conditions of high summer temperatures.

With diploids, tetraploids, and hexaploids available which are not ecologically bound to sandy soils and high water tables, and which are not injured by high summer temperatures, one of the first steps taken in a breeding program is an attempt to enlarge the range of habitat and conditions under which commercial blueberries might be successfully grown. So far, results have been most encouraging.

Like most plants, blueberries are subject to a series of diseases and pests which, under plantation conditions, may become epidemic. While only a beginning toward the production of resistant stock has been made, even a casual examination of any field planting shows marked differences in resistance to the attacks of various pests and diseases, within the same blueberry

species and among the different hybrid combinations. For example, the Black Giant, a variety of *V. ashei*, is fully resistant to stem canker, while adjacent seedlings of the same species have been killed outright by this disease. Such differences suggest the reason that insect and disease resistance is a major part of any breeding program.

In addition to the production of new varieties of blueberries for table use, the group has other potentialities. Among these are its possibilities in soil conservation and wild-life management. Because of the vigorous growth of certain species and their production of extensive colonies by means of interlaced stolons, they may be suited for combating erosion and checking various types of gullying under certain conditions. Furthermore, there is no reason why these same plants should not provide fruit of excellent quality for at least local consumption. Steps already have been taken to provide just such material. It is suggested that certain of these types might also be suitable for use where contour strip and terrace farming are practiced. So far as song birds, game birds, and the smaller animals are concerned, there is scarcely any better cover than a blueberry thicket; nor need we consider only the smaller animals, for every woodsman knows the relation of blueberries to bears; and the plants also furnish excellent browse for deer.

The ornamental possibilities of the group cannot be passed over lightly. Although no particular attempt has been made in our work to develop material especially adapted to ornamental purposes, chance combinations have yielded plants of considerable beauty and grace. There are clones which are unusually large-flowered, some with cascades of pearly white bloom; others are pink, and still others deep red. To those of us who have seen them, the glossy beauty of the *V. australe*  $\times$  *myrsinites* hybrids is a thing never to be forgotten. And there is scarcely a plant more intriguing than a carefully tended specimen of the dwarf and evergreen *V. myrsinites* as it unfolds its new set of minute leaves and delicate pink flowers. There is now available for further development material that can add gaiety to the spring scene in our gardens because of its splendid trusses of flowers. In midsummer, the deciduous species add a note of stately grace with their arched branches and glossy leaves. And where is there a shrub more striking than *Vaccinium atrococcum* standing in the low sunlight of an autumn afternoon wrapped in its cloak of crimson leaves? Southward, the evergreen plants lend their own peculiar cheer to the winter aspect of gardens and lawns. And the interesting thing is: All of them yield a most delectable crop of food, either for ourselves, or for the feathered guests around our homes. As a group of potential ornamentals, the blueberries have been sadly neglected.

#### SUMMARY

The blueberries, a floristically and horticulturally important group in eastern North America, are characterized by two outstanding cytogenetic



features: (1) the abundance of polyploids and (2) the rarity of well-marked sterility barriers between homoploids. These two factors, more than any others, have been responsible for the production of morphologically complex populations, and have added to the difficulties of providing an adequate taxonomic treatment along orthodox lines. Conversely, these same factors have been of paramount assistance to those seeking to develop new horticultural material in the group.

The present paper serves to indicate the ease with which hybrids may be produced between individuals of homoploid species under controlled conditions. And the fact that these hybrids, for the most part, are completely fertile further indicates that the majority of the natural populations suspected of being of hybrid and segregate origin have been produced in this manner.

An annotated list of the suspected hybrid combinations observed in the wild is presented. In many instances, these have been duplicated under controlled conditions; in others, the plants thought to be hybrids on purely morphological grounds have been checked and found to be homoploid with species growing in the same region, which species must have furnished the parental material.

The following factors are thought to be responsible for the numerous populations of wild interspecific hybrids present today in the genus: (1) the absence of effective sterility barriers between most homoploids; (2) the presence of a considerable amount of self-sterility; (3) pollination, mostly effected by bees; (4) an early flowering season, when other nectar-bearing species are comparatively scarce; (5) seed distribution, accomplished mostly by birds; (6) the longevity of clones, giving ample time for chance cross-pollination and also (7) permitting individual plants to persist in advantageous micro-habitats in the face of ecological changes; (8) the widespread distributional adjustments of the North American species following the disturbances of the Pleistocene and more recent post-Pleistocene xeric period, permitting them to make ecological contact; (9) the ability of many species to migrate into and become established in areas disturbed by man; and (10) the reluctance of man to destroy a plant which furnishes food and financial remuneration to himself, as well as food and cover for many of his favorite game-birds and wild animals.

Although fields of lowbush blueberries in the northeastern States have been given some special cultural attention for nearly a century, and the high-bush varieties have been grown commercially in the United States for about 25 years and notable progress made in the selection and breeding of new forms, the marked horticultural advances of the last few years have been made possible only by an increased knowledge of the cytogenetic and biological situations underlying the group.

The importance of blueberries is pointed out, not only as a source of food, but also as effective agents in erosion control, as wild life cover, and for ornamental effect.

The present paper closes with a survey of the more important factors to be considered in further improvement, together with brief mention of the results achieved up to the present. Important as the recent improvements may seem to be, the writers are convinced that only a beginning has been made.

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**DRYOPTERIS, DESCHAMPSIA, PORTULACA, LUPINUS,  
FAGARA, STENOGYNE, AND DUBAUTIA.  
HAWAIIAN PLANT STUDIES 12<sup>1</sup>**

HAROLD ST. JOHN

POLYPODIACEAE

*DRYOPTERIS GOGGILODUS* (Schk.) Kuntze emend. Fosberg. In 1942 Fosberg published *D. goggilodus* as a new combination (Bishop Mus., Occ. Pap. 16: 337-338, 1942). It was based on the original *Aspidium goggilodus* Schkuhr (1809), which had been given an altered spelling when transferred as *Cyclosorus gongylodes* (Schk.) Link (1833). As Fosberg indicates, Link's specific name was an alteration or orthographic variant of the original one by Schkuhr. Subsequent authors generally accepted this altered spelling and placed the species in the generic unit then current. As Fosberg points out, it is now necessary to adopt the original spelling of the specific name, that is *goggilodus*. Though its latinization may be dubious, still the specific name was not an unintentional orthographic error. Hence, the original spelling must be accepted.

The combination *Dryopteris gongylodes* (Schk.) Kuntze (1891) was not an independent new species. It was a transfer based upon *A[spidium] gongylodes* Schkuhr. Kuntze, thus, accepted Link's altered spelling of the specific name, but clearly made a new combination in *Dryopteris* based upon the original *A. goggilodus* Schk. There were no generally accepted rules of nomenclature during Kuntze's time. He was a zealous reformer and published book after book filled largely with orthographic alterations of the binomials published by earlier botanists. Use of the exact original spelling was to him less important than having a name etymologically correct by his own standards. Hence, he proceeded to "reform" thousands of valid names published by previous botanists. Today we do taxonomic work in conformity with the detailed articles and recommendations of the International Rules of Botanical Nomenclature. Articles 59 and 70 interdict the reformation of botanical names on such grounds as their being badly chosen. Hence, the original spelling must be used, unless it was demonstrably an unintentional orthographic error. Schkuhr's name was not such an error. Fosberg now accepts the original spelling of the specific name, and places it under *Dry-*

<sup>1</sup> This is the twelfth of a series of papers designed to present descriptions, revisions, and records of Hawaiian plants. The preceding papers have been published as Bishop Mus. Occ. Papers 10(4), 1933; 10(12), 1934; 11(14), 1935; 12(8), 1936; 14(8), 1938; 15(1), 1939; 15(2), 1939; 15(22), 1940; 15(28), 1940; and no. 11 is in press. The specimens cited, including the new types, are in the herbarium of the Bishop Museum, Honolulu.

*opteris*, which seems the correct generic disposition. Earlier, Kuntze made the same combination, except that he used the modified spelling of the specific name, though basing it on the original Schkuhr species. These two names, *Dryopteris gongylodes* (Schk.) Kuntze and *Dryopteris goggilodus* (Schk.) Fosberg are to be considered orthographic variants of the same name. They are comparable to the examples given in the rules under Article 70: *napaulensis*, *nepalensis*, *nipalensis*, or *chinensis*, *sinensis*, or *ceylanica*, *zeylanica*. Hence, *gongylodes* was not a new name distinct from *goggilodus*, but a mere orthographic variant and there was no need of proposing a new combination under *Dryopteris*. The proper name was available, needing only an etymological alteration back to the original spelling. It now should stand as *Dryopteris goggilodus* (Schkuhr) Kuntze emend. Fosberg.

## GRAMINEAE

The native Hawaiian species called by Hillebrand *Deschampsia* were placed by Skottsberg in the genus *Aira*. For several decades there was a taxonomic and nomenclatorial confusion between these two genera and *Aspris*. Now this has been settled by the selection of *Aira praecox* L. as the lectotype of the genus *Aira* (Internat. Rules Bot. Nomencl. ed. 3. 139. 1935). This generic name is thus stabilized for the species without prolongation of the rhachilla and with the lemmas terminating in two slender teeth. Then, there is no need of the generic name *Aspris* which becomes a synonym of *Aira*. *Deschampsia* when first described contained many species now considered of several genera. When the various generic segregates were removed, the plurality of species were representative of *Deschampsia* as traditionally accepted for the species with the rhachilla prolonged behind the upper floret, and the lemmas truncate, erose-dentate at summit. Hitchcock in his Grasses of Hawaii (Mem. Bishop Mus. 8(3): 143-145. 1922), when following the American Rules, placed the native Hawaiian species in *Aira*. Now, under the International Rules, these species with prolonged rhachilla and truncate lemmas should be placed in *Deschampsia*.

***Deschampsia hawaiiensis*** (Skotts.) St. John, comb. nov. *Aira hawaiiensis* (Hillebrand herb.) Skotts. Medd. Göteborgs Bot. Trädgård 2: 205-207. f. 1b, c. 1926. *D. australis* Hillebrand, Fl. Haw. Is. 520-521. 1888; not Raoul, 1846.

**DESCHAMPSIA HAWAIIENSIS** (Skotts.) St. John, f. ***depauperata*** (Skotts.) St. John, comb. nov. *Aira hawaiiensis* (Hillebrand herb.) Skotts. f. *depauperata* Skotts. Medd. Göteborgs Bot. Trädgård 2: 207-208. 1926.

**DESCHAMPSIA HAWAIIENSIS** (Skotts.) St. John f. ***haleakalensis*** (Skotts.) St. John, comb. nov. *Aira hawaiiensis* (Hillebrand herb.) Skotts. f. *haleakalensis* Skotts. Medd. Göteborgs Bot. Trädgård 2: 207. 1926.

## PORTULACACEAE

*PORTULACA CYANOSPERMA* Egler, Bishop Mus. Occ. Pap. **18**(15): 167-170. 1937.

OAHU: Waianae, dried alluvial flat, north of Mauna Kuwale, alt. 300 ft., Nov. 11, 1941, Mrs. Juliette Oliviera Wentworth.

The specimens were transplanted and cultivated in Honolulu. They were grown in pots at the Pineapple Research Institute. Those placed outdoors in the sun became depressed but with many vigorous branches; the crowded leaves 7-21 mm. long, 1-4 mm. wide, flattened, linear to narrowly oblance-linear, and mostly strongly tinged with red; and the flowers abundant. Those grown in the greenhouse were more or less erect, of loose growth; the remote leaves 12-33 mm. long, 1-3 mm. wide, flattened, linear; and the flowers few. The flowers open about 10 a.m. and close in the early afternoon. Herbarium specimens were made from these July 31, 1942. They differ from the characters given by Dr. Frank E. Egler only in having the hairs subtending the flowers only 5-7 mm. long instead of 1 cm. long. This is not deemed of importance, especially as Egler himself demonstrates the variability in length of the hairs in the leaf axils, averaging about 5 mm. in length.

The color of the petals was Phlox Purple (Ridgway, R., Color Standards and Color Nomenclature pl. 11, 1912) or (Maerz, A. & Paul, M. R., Dictionary of Color pl. 52, 12E, 1930).

The species was previously known only from the islands of Lehua and Kauai. Hence, this Oahu locality is an interesting range extension. The potted plants seed prolifically and scatter their seeds around. They have seeded in this way the vicinity of the spots where they have been cultivated in Honolulu. Mrs. Wentworth assures the writer that there is no possibility that the plants growing naturally in the arid western part of Oahu at Waianae could have in any way sprung from the Lehua plants cultivated on the opposite side of the island in Honolulu by Caum and Egler.

## LEGUMINOSAE

*LUPINUS ALBUS* L. var. *TERMIS* (Porsk.) Alefeld. "Lupine," "Tremogo" (Portuguese).

MAUI: Haiku Uka, Olinda, 3,800 ft. alt., cult., Aug. 4, 1943, H. St. John 20,359.

The plant is vigorous, from 1-1.8 meters tall, with blue flowers and abundant, large pinkish seeds. The seeds after leaching for a week are cooked and eaten by the Portuguese.

## RUTACEAE

*FAGARA DIPETALA* (Mann) Engler var. *geminicarpa* (Rock) St. John, comb. nov. *Xanthoxylum dipetalum* Mann. var. *geminicarpum* Rock, Ind. Trees Haw. Is. 209-210. pl. 81-83. 1913.

FAGARA MAUIENSIS (Mann) Engler var. **anceps** (Rock) St. John, comb. nov., f. **petiolulata** (Rock) St. John, comb. nov. *Xanthoxylum mauiense* Mann var. *anceps* Rock f. *petiolulatum* Rock, Ind. Trees Haw. Is. 205-206. 1913.

## LABIATAE

**Stenogyne mollis** (Sherff) St. John, comb. nov. *S. rugosa* Benth. var. *mollis* Sherff, Bot. Gaz. **96**: 141-142. 1934.

This was published as a variety and briefly diagnosed by Sherff in 1934; later in his monograph (Bishop Mus. Bull. **136**: 67-68. 1935) he cited numerous collections of it. It is a characteristic plant of the western slope of the island of Hawaii, occurring at Waikii on the side of Mauna Kea, on Hualalai, and abundantly in Kona.

It differs markedly from *S. rugosa* in its abundant uniform pubescence; in the calyx lobes all shorter than the tube and oblong or oblong-lanceolate and merely acute, not subulate, tipped; and in the corolla shorter, only 12-15 mm. long. *S. rugosa* is sparsely hirsute to glabrate; the calyx sparsely hirsute or glabrous; the calyx lobes lanceolate, acute and subulate tipped; and the corolla 14-22 mm. long. This latter species occurs on both east and west sides of the island of Hawaii. Since the var. *mollis* has numerous and constant characters that seem to be adequate and diagnostic, and as it has a different range, it is here raised to specific status.

STENOGYNE RUGOSA Benth. *S. rugosa* Benth. var. *subulata* Sherff, Bot. Gaz. **96**: 142. 1934; Bishop Mus. Bull. **136**: 68. f. 22. 1935. *S. kaalae* Wawra var. *coriacea* Degener & Sherff ex Degener, Fl. Hawai. fam. 316. 13 S 1935.

*Stenogyne kaalae* var. *coriacea* is maintained by Sherff in his monograph of the genus (Bishop Mus. Bull. **136**: 76. 1935). Cotype material and more recent collections from Kilauea, Hawaii, *Fagerlund & Mitchell* 3, and 15, can easily be run through Sherff's key to var. *coriacea*. This was keyed on the purely numerical basis of whorls 2-flowered, versus whorls 6- (or 2-4-8-10) flowered. Comparison shows that var. *coriacea* of the island of Hawaii differs from *S. kaalae* of the Waianae Mts., Oahu, in aspect and in leaf shape, toothing, short pubescence, calyx and corolla pubescence. It does not seem most closely related to that species. Further comparison shows it to be identical with *S. rugosa* var. *subulata* of the island of Hawaii. Single branches of var. *coriacea* have the whorls 2-, 4-, or 6-flowered, and this was well shown in the original illustration in Degener's Flora Hawaiiensis. The var. *coriacea*, since it agrees in structure, is not separable from *S. rugosa* var. *subulata*.

A reexamination of *S. rugosa* and its var. *subulata*, using specimens cited by Sherff, reveals a different status of the diagnostic characters, as follows: *S. rugosa* has the petioles 3-22 mm. long; blades 1.7-9.3 cm. long, 1-4 cm. wide, from narrowly oblong-lanceolate to lanceolate and ovate, acute; calyx

lobes subequal to the tube, lanceolate, acute or subulate tipped. The var. *subulata* has the petioles 5–17 mm. long; blades 2–7 cm. long, 0.8–2.8 cm. wide, from narrowly oblong-lanceolate to lanceolate and ovate, acute; calyx lobes subequal to the tube, lanceolate, acute or subulate tipped.

The leaves are of various shapes, but several such are to be found on a short section of a stem. The larger and broader leaves are usually on the main or ascending branches, while the narrower blades occur on smaller lateral branches or more often on prostrate, weak branchlets. The calyx is accrescent from bud to fruit, increasing materially in size. Its orifice is markedly oblique, with the upper tooth much shorter than the lateral or especially the lower ones. A contrast made between the length of calyx tube and calyx teeth without qualification as to which teeth were examined is of little value. Actually the upper tooth is much shorter than the tube, the lateral teeth are subequal to it, and the lower teeth exceed it in length. There are no discernible differences in pubescence of petiole. The leaves show the same gamut of shapes in both. The calyx shape and toothing is identical. From the expanded measurements given here, it will be seen that some individuals of *S. rugosa* have somewhat longer petioles, longer and wider blades, but the measurements largely overlap and the fact that some specimens of the species are slightly larger in size of their largest blades may be correlated with the fact that the specimens of it are more numerous than those of the variety. This new study of the specimens and reevaluation of the characters indicates clearly that the variety *subulata* Sherff has no diagnostic differences, so it is here placed in the synonymy of *S. rugosa* Benth.

#### COMPOSITAE

DUBAUTIA PLANTAGINEA Gaud. var. *typica* St. John, var. nov. *D. plantaginea* Gaud. Voy. Uranie Bot. 468. 1830; Atlas pl. 84. 1830. *D. plantaginea* Gaud. var. *Chamissonis* Sherff, Am. Jour. Bot. **20**: 616. 1933; Bishop Mus. Bull. **135**: 86–87. f. 29. 1935. *D. plantaginea* Gaud. var. *angustifolia* Sherff, Am. Jour. Bot. **20**: 616. 1933; Bishop Mus. Bull. **135**: 187–188. 1935.

Sherff pointed out that Gaudichaud's illustration of *D. plantaginea* showed a panicle with markedly alternate branches. This character was also mentioned in Gaudichaud's brief description. Sherff matched the illustration with two collections from the island of Lanai and removed all specimens from Oahu from the species proper, thus differing from the interpretations of previous botanists. He described the Oahu specimens as var. *Chamissonis* Sherff which was said to differ by having the "Principal branches of the panicle opposite."

For some time the writer has intended to check over this group, for it is well known that the Urania Voyage did not visit Lanai, so Gaudichaud could not have collected a species restricted to the mountains of that island.

The only subsequent collections from Lanai, accepted by Sherff as *D. plantaginea*, are in the Bishop Museum and are at hand. *Munro* 48, Dec. 23, 1913, Lanaihale, has one flowering branch. Its stem is swollen and blighted at apex, is clearly diseased, and perhaps injured by a borer. From the uppermost axils it bears four slender, spindly branches. One is vegetative but produces only shortened, lanceolate, bract-like leaves. The other three are flowering, one with buds, the other two with flowers and fruit. The panicles are reduced, 8–12 cm. long, 5–7.5 cm. wide, and the lower and principal branches are alternate. On the sheet is another stem, also blighted at tip, but its axillary branchlet is vegetative with normal, linear-oblong leaves 11–12 cm. long, 18–22 mm. wide.

The remaining modern collection is also from Lanai, Waiopaa, *G. C. Munro* 271. Its flowering specimen is also on a stem swollen and blighted at the apex. Just below this blighted apex, spring two axillary branchlets, slender, but fairly well developed, and bearing fruiting panicles 7.5–8 cm. long, 4–6 cm. wide, the principal branches of which are alternate or subopposite. Thus it is found that the only two modern collections accepted by Sherff as matching exactly Gaudichaud's type from the *Uranie* Voyage are two specimens with injured main stems, and reduced panicles produced on the weak secondary branchlets. Gaudichaud's illustrations are often more revealing of details than the brief Latin diagnoses. For years I have used his book and I have compared it with the types in Paris, and with fresh, living specimens in the Hawaiian Islands. The steel engravings are striking, bold, and attractive, but in fine detail, particularly of pubescence, they are often inaccurate. On gross detail they are excellent. There is no explanatory statement, but I have concluded that nearly all the habit drawings were made life size. The inflorescence of *D. plantaginea* is shown as 16 cm. long and 10.5 cm. wide. This agrees well with the sizes of normal plants on Oahu or Lanai, but not with the ones from weak secondary branchlets, as in the two cited by Sherff as typical. He gave the measurement as " $\pm 1$  dm. long." Hence, the size of the inflorescence cannot be used as a sound diagnostic character.

Sherff gives the ranges as *D. plantaginea* from Lanai; while the var. *Chamissonis* as from Kauai, Oahu, Maui, and Hawaii. He must have made an oversight, for in his revision, p. 87, under Specimens examined, he cites three collections from the island of Lanai: *Forbes* 284.L; *Forbes* 299.L; and *Munro*, Nov. 11, 1916. One is vegetative, but the others are in bud or flower. In the most mature one, *Munro*, Nov. 11, 1916, the panicle is 15 cm. long, 20 cm. wide. In stem, leaf, and inflorescence, it is a good match for the Oahu plants. The branches of the inflorescence are opposite. There is another, more recent, Lanai fruiting specimen now at hand, Kaiholena Gulch, *F. R. Fosberg* 12,505. Its inflorescence is 15 cm. long and about 12 cm. wide.



The collections of var. *Chamissonis* have been studied to test the constancy of opposite branching of the inflorescence. The great majority have the inflorescence with the lower and median branches opposite, but towards the tip there is a change to subopposite or commonly to alternate. With this as the mean, it is not surprising to find exceptions. The following collections from Oahu, and all but the first and last cited by Sherff, have the lower one to three nodes producing alternate branches. These are, from the Waianae Mts.: Puu Kaala, *St. John* 9,925; Puu Kaala, *Fosberg* 10,363; Mt. Kaala, Nov. 13, 1929, Y. Tanaka; Puu Kaula, *Fosberg* 9,007; from the Koolau Range: Pauoa, *Garber* 140; and Kipapa Gulch, *Hosaka* 1,242. It is concluded that alternate branching of the inflorescence is occasional, especially on weak secondary branchlets. In any case, it is not constant, and it does not appear significant.

The only remaining differences mentioned by Sherff are: *D. plantaginea* having the leaves "at base more or less widened and clasping the stem"; var. *Chamissonis* having the leaves "more or less narrowed toward base and semi-amplexicaulous." This sounds like the recognition of a broad leaved and a narrow leaved variant. Close study of the many cited specimens and of others shows no difference whatever. The qualifying phrase "more or less" seems to make the words widened and narrowed, quite meaningless, as used by Sherff.

The geographic range of var. *Chamissonis* Sherff was carelessly handled by Sherff. His half page of Specimens examined, lists many from Oahu and three from Lanai. His summary of range is:

"Distribution: islands of Kauai, Oahu, Maui, and Hawaii." He failed to include Lanai, instead adding to Oahu the islands of Kauai, Maui, and Hawaii for which no collections were cited, nor are any now known to the writer. Sherff's method of citing collections alphabetically under the collectors may be convenient for him, but it obscures all geographic correlations and gives the user the very tedious task of scanning every line if he seeks information on where the plant grows. Then, if Sherff's summary of distribution is wrong, as in this case, it may go undetected for years.

In summary, the characters given for var. *Chamissonis* Sherff are either nonexistent or lacking in significance. Gaudichaud could not have collected the type of *D. plantaginea* on Lanai because he did not visit that island. The Lanai plants prove to be inseparable from the Oahu ones. Hence, var. *Chamissonis* is reduced to the synonymy of *D. plantaginea* Gaud.

*Dubautia plantaginea* Gaud. var. *angustifolia* Sherff was described in 1933 and given a 1½-line diagnosis and a type citation. In 1935 Sherff in his subsequent revision gave a 2-line description in English, an exact translation of the Latin diagnosis except for the added words: Leaves narrowed below, more elongate. Besides the type he cited eleven other collections. Eight of

these are before me. The key characters agree with the details given in the description :

- a. Principal leaves 1-2 dm long and commonly 1-3.4 cm wide - - - -
- a. Principal leaves about 1.2-1.9 dm long and 0.7-1.3 (rarely -1.6 cm wide - - - - -  
variety  $\gamma$  *angustifolia*

Neither a first nor a repeated reading of those lines will reveal any tangible key characters. A key should single out the diagnostic differences, but this one fails to do so. The making of keys is an art, well mastered by some botanists, but not by others. The excellence of the key is a good test of the finished quality of taxonomic work. There are numerous similar stumbling blocks in the keys in the now numerous, hurried revisions of Hawaiian genera by Sherff. These treatments and keys have proven to be the despair of students of the Hawaiian flora.

These critical remarks do not dispose of var. *angustifolia* Sherff. The name is valid and it was effectively published. Even though its key character is worthless, it still might have distinctive characters and be a good variety. It is recorded on Oahu from Mt. Kaala in the Waianae Mts.; and in the Koolau Range from the Waikane-Schofield trail to Puu Konahuanui. The closest relative, as treated by Sherff, is the var. *Chamissonis* Sherff which also occurs in the same zone at every one of the recorded localities. Hence, var. *angustifolia* has no distinct geographic range. The latter variety was stated to have more elongate bracts of the inflorescence. Comparison with the very numerous specimens of var. *Chamissonis* reveals that this is not so, and not even a tendency towards longer bracts is detectable. There remains only the alleged leaf character, its size and particularly its width. The type specimen of var. *angustifolia* from Nuanu, Oahu, Sept. 1860, Hillebrand (Kew) has not been available, but a satisfactory judgement seems possible from the eight paratypes at hand. The specimens of var. *Chamissonis* labeled and cited by Sherff show some with narrow, some with intermediate, some with broader principal leaves. The minimum width is 1 cm. and the maximum 3.4 cm. Between these extremes are all gradations. Some of those with the narrowest leaves were separated as var. *angustifolia*, but not all. The two following, studied and cited by Sherff as var. *Chamissonis* have all the appearance of and are inseparable from his var. *angustifolia*. These are, Oahu : Pauoa, *Rock 1055*; and Waiolani, *Forbes 1848.0*. As in any species population there are extremes between which the leaves of individuals show fluctuation. This is so here. There is a range of fluctuation from narrow to broad extremes. There is no perceptible break in the series. Regardless of the inadequacy of Sherff's key, the narrower leaved plants are not separable on having leaves less than 1.9 cm. wide or at any other figure. There is such a complete fluctuation in leaf width; there are no other known characters; there is no geographic separation; so that it is clear to the writer that var. *angustifolia* must be

merged with var. *Chamissonis* which as demonstrated itself becomes a synonym of *D. plantaginea* Gaud.

For a species with numerous varieties, it is helpful to have the original sort given a name, such as var. *typica*.

DUBAUTIA PLANTAGINEA Gaud. var. *STRIGOSA* Skotts. Medd. Göteborg Bot. Trädgård **2**: 277. 1926; sensu Sherff, Bishop Mus. Bull. **135**: 88. 1935, as to specimens from the island of Hawaii, not as to those from Maui and Oahu.

Leaves below appressed pilose; involueral bracts 5–5.5 mm. long, the back short capitate glandular and towards the tip sparsely hirsutulous, the margin sparsely hirsutulous ciliate towards the tip.

TYPE: island of Hawaii, Kohala Mts. above Kamuela (Waimea), 1,100 m., Sept. 29, 1922, *C. Skottsberg* 733 (Ho.).

*Specimens examined*: all from Hawaii, Kohala, W. Hillebrand & J. M. Lydgate; Kohala Mts., Waimea, Sept. 7, 1911, *C. N. Forbes* 190.II; Hualalai, Puuli crater, 5,000 ft., June 11, 1909, *J. F. Rock* 3,679 (217).

The two following varieties are described on material included by Sherff in his concept of var. *strigosa* Skotts.

DUBAUTIA PLANTAGINEA Gaud. var. *pauoaensis* St. John, var. nov.

Foliis infra adpressi-pilosulis, bracteis involucri 4–4.5 mm. longis dorso sparse puberulenti deinde subglabrato marginibus puberulo-ciliatis apicem versus.

TYPE: Oahu, Pauoa Valley, Jan. 8, 1910, *J. F. Rock* 215 (Ho.).

DUBAUTIA PLANTAGINEA Gaud. var. *glandulosa* St. John, var. nov.

Foliis infra adpressi-villosis, bracteis involucri 3.8–4.3 mm. longis, ad basim capitato-glandulosis et remote hirsutis, dorso glabro, marginibus dense pilosuli-ciliatis.

TYPE: Eastern Maui, Kahikinui, Oct., 1910, *J. F. Rock* 8,652 (Ho.).

*Specimens examined*: all from Maui, South Haleakala, Ex Museo botanico Berolinensi, presumably by W. Hillebrand; south slope of Haleakala, east of Puu Pani [= Puu Pane], sterile tree, 12 ft. high, March [= April] 4, 1920, *C. N. Forbes* 2,135.M.

UNIVERSITY OF HAWAII

THE JATROPHAS OF CERVANTES AND OF THE  
SESSÉ & MOCIÑO HERBARIUM

ROGERS McVAUGH

Among the several hundred species names published in the genus *Jatropha*, of the Euphorbiaceae, are 8 published in 1794, with brief descriptions, by Vicente de Cervantes, who at that time held the chair of Botany in the Royal Botanical Garden in Mexico City. All these names relate to Mexican species, but are so briefly characterized as to make their identification all but impossible from the descriptions alone, and none of them is currently applied to any known species of *Jatropha*. It is now possible, however, to associate most of Cervantes' names with definite species, on the basis of contemporaneously named specimens from the herbarium of Sessé & Mociño, now on deposit at the Field Museum.

To Mr. Paul C. Standley of the Chicago Natural History Museum (Field Museum), who read this paper in manuscript, I am very grateful for his assistance in locating and assembling the numerous specimens involved, for his suggestion that some of the supposed species of *Jatropha* were in reality species of *Manihot*, and for his kindness in supplying some of the historical details in reference to the collection of Sessé and Mociño.

Cervantes, who was a member of the Botanical Expedition headed by Sessé which was sent to New Spain by Charles III, was Professor ("Catedrático") in the Royal Botanical Garden from 1788 until 1820 and perhaps until his death in 1829.<sup>1</sup> The most detailed account in English of his work and that of the other members of the Expedition to Mexico is that by Standley (Contr. U. S. Nat. Herb. **23**: 13-18. 1920). He seems to have devoted most of his time to his professorial duties, for although he was rather well known to European botanists through correspondence, his published works were few. He was the author of a few short papers in the *Anales de Ciencias Naturales*, and his comprehensive account of the Central American rubber tree was published as a 35-page supplement to *La Gazeta de Literatura* [volume 3], on July 2, 1794, with the title: "Discurso pronunciado en el Real Jardín Botánico el 2 de Junio por el Catedrático Don Vicente de Cervantes"; this paper was translated into English and published in abridged form in 1805, in König's *Tracts Relative to Botany* under the title of "Account of the Ule-tree (Castilla elastica), and of other trees producing the

<sup>1</sup> Dr. H. W. Rickett supplies information that records of the Botanical Garden in the National Archives of Mexico cease with the year 1820.

elastic gum." The "other trees producing the elastic gum" included several *Jatrophas*, of which Cervantes (1794, p. 3) wrote:

"En las tierras calientes de este Reyno abundan muchas especies del mismo género *Yatropha*, como son la *mala Muger*, (3) el árbol de los *Piñones de Indias* (4) y otras varias especies conocidas (5) y nuevas (6) descritas por el citado Señor Director [i.e. Sessé, to whom Cervantes has just referred as Don Martin de Sesé y Lacasta] en la Flora Mexicana.

"(3) *Jatropha urens*.

"(4) *J. Curcas*

"(5) *Manihot*. Jan J. *Janipha*. J. *Herbacea* Linn.

"(6) [Here follow the descriptions of the 8 newly proposed species]."

From the above it seems clear, as Sprague (*Kew Bull.* 1926: 418. 1926) has already suggested, that the descriptions published by Cervantes were taken directly from the projected but unpublished *Flora Mexicana* of Sessé and Mociño; additional evidence for this may be found in the descriptions themselves, all of which end with a citation of "Flor. Mex." or "Flor. Mex. cum icone."

Most of the specimens in the herbarium of Sessé and Mociño were identified by them, at least to the genus; where possible, they identified their plants with Linnean species or those of the few other authors available to them. When they deemed this impossible, their specimens were designated by manuscript names which were intended for publication in the *Flora Mexicana*, these names often being accompanied by "N." [for "Nobis"] or "ic." [referring to one of the plates for the flora]. The *Jatrophas* (including *Cnidoscolus*) in their collection are similarly labelled and are listed below, arranged according to the arbitrary numbers assigned the specimens at Madrid:

Number	Identity of Specimen	Notation by Sessé & Mociño
4220	<i>Jatropha gossypifolia</i> var. <i>elegans</i> (Pohl) Muell. Arg.	" <i>Jatropha gossypifolia</i> ."
4221	<i>Jatropha cathartica</i> Ter. & Berl. [ <i>J. Berlandieri</i> Torr.].	" <i>Jatropha</i> <sup>2</sup> . . . N. Communicavit et misit D. Ignatius Leon."
4223	<i>Jatropha multifida</i> L.	" <i>Jatropha multifida</i> . ic."
4225	<i>Cnidoscolus Chayamansa</i> McVaugh.	" <i>Jatropha urens</i> ."
4226	<i>Jatropha olivacea</i> Muell. Arg.	" <i>Jatropha ciliata</i> N. <i>Jatropha foliis lobatis ciliato-glandulosus</i> ."
4227	<i>Cnidoscolus tubulosus</i> (Muell. Arg.) Johnst. [ <i>Jatropha tubulosa</i> var. <i>septemloba</i> Muell. Arg.].	" <i>Jatropha quinqueloba</i> N. <i>Jatropha foliis palmatis 5-lobis dentatis inermibus basi biglandulosus</i> ."
4228	<i>Manihot foetida</i> (H.B.K.) Pohl.	" <i>Jatropha triloba</i> N. <i>Jatropha foliis trilobis integerrimis</i> ."
4229	<i>Manihot foetida</i> (H.B.K.) Pohl.	" <i>Jatropha</i> <sup>3</sup> . . . N. <i>peltata</i> ."
4230	<i>Manihot</i> sp.	" <i>Jatropha palmata</i> N. <i>Jatropha foliis palmatis lobis obtusis integerrimis</i> ."
		" <i>Arbuseula</i> 15 ped. Flores nudi."
4231	<i>Jatropha podagrica</i> Hook. and ? <i>Jatropha platyphylla</i> Muell. Arg.	" <i>Jatropha peltata</i> N. ic."

<sup>2</sup> Specific name never published in this genus.

<sup>3</sup> Unpublished specific name crossed out "peltata" substituted.

Number	Identity of Specimen	Notation by Sessé & Mociño
4232	<i>Cnidoscolus angustidens</i> Torr.	" <i>Jatropha herbacea</i> . <i>Jatropha aculeata</i> foliis trilobis dentato-sinuatis, caule herbaceo. Radix tuberosa lactescens. Caul. sesquiped."
4233	<i>Jatropha Curcas</i> L.	" <i>Jatropha edulis</i> N. ic."
4234	<i>Jatropha</i> sp., near <i>J. Alamani</i> (leaf only).	" <i>Jatropha curcas</i> ."
4235	<i>Jatropha</i> sp., near <i>J. Alamani</i> .	" <i>Jatropha</i> ."
4236	<i>Jatropha</i> sp., near <i>J. Alamani</i> (leaves only).	" <i>Jatropha curcas</i> ."
4237	<i>Jatropha Alamani</i> Muell. Arg.	" <i>Jatropha curcas</i> ."
4238	<i>Jatropha spathulata</i> var. <i>sessiliflora</i> (Hook.) Muell. Arg.	" <i>Jatropha dioica</i> N. ic. Vgo. Sangre de drago."
4243	<i>Jatropha hastata</i> Jacq. [ <i>J. integririma</i> Jacq.].	" <i>Jatropha molucensis</i> . Havan. Peregrina."
4244	<i>Jatropha cinerea</i> (Orteg.) Muell. Arg., and <i>Jatropha cordata</i> (Orteg.) Muell. Arg. <sup>4</sup>	" <i>Jatropha moluccana</i> ."
4245	<i>Jatropha cordata</i> (Orteg.) Muell. Arg.	" <i>Jatropha</i> <sup>2</sup> . . . N."
4246	<i>Jatropha hastata</i> Jacq. [ <i>J. integririma</i> Jacq.].	" <i>Jatropha moluccana</i> ic."
4247	<i>Jatropha hernandiacfolia</i> Vent. and <i>J. hastata</i> Jacq. <sup>5</sup>	" <i>Jatropha heterophylla</i> N."

It will be seen that the authors of the comments and notes quoted above used six Linnean names, evidently with full knowledge of their origin; in addition to these, their herbarium contained ten species which they considered new to science, and for which they intended to propose new names. One of these (*Jatropha heterophylla*) was published in the *Flora Mexicana* (ed. 2. 224. 1894); two of them seem never to have been published; the remaining seven were published, not in the ill-fated volumes which appeared under the names of Sessé and Mociño late in the 19th century, but by Cervantes in 1794! Cervantes' descriptions, although brief and unsatisfactory, are sufficiently diagnostic to make it clear that they apply to the species in question, those labelled with his names in the herbarium of Sessé and Mociño.

Parenthetically it may be pointed out, with reference to the above table, that the name *Jatropha molucensis* (Fl. Mex. ed. 2. 224. 1894) was probably never intended for publication, being evidently a misprint for *molucensis* (see no. 4243 above), which in its turn seems to have been carelessly used in place of *moluccana*, the Linnean name which the authors understood to apply to the plant we know as *Jatropha hastata* Jacq. Since the name *molucensis* was published, however, this specimen may be taken as the type.

<sup>4</sup> A single leaf of *J. cordata*, quite possibly derived from no. 4245.

<sup>5</sup> A portion of an inflorescence of *J. hastata*, quite possibly derived from no. 4246. *J. heterophylla* is to be typified by the other element.

With this corroboration from herbarium specimens, we are probably justified in supposing that the Sessé and Mociño plants are to be regarded as the types of Cervantes' species, since there are no apparent discrepancies between the specimens themselves and the published account, either in names or in descriptions. It is necessary to make the reservation that in the Sessé and Mociño herbarium as it has come down to us there are some known additions and mixtures and misplaced data, so that we are not always able to associate names and specimens with entire confidence; in these particular cases, however, our assumptions appear to be justified.

Since Cervantes definitely named Sessé as the author of the descriptions, the species are to be attributed to him rather than to Cervantes. A formal discussion of the 8 species follows:

1. *JATROPHA PELTATA* Sessé apud Cerv. Gaz. Lit. Mex. **3**: supl. 3. 1794; König, Tracts Bot. 231. 1805. The original description reads: "*Jatropha* (*Peltata*) floribus caliculatis, folijs peltatis. Flor. Mex. cum icone." This plant, if actually a *Jatropha* and a Mexican or Central American species, can be nothing except *J. podagrica* Hook. or *J. platyphylla* Muell. Arg. Among the Sessé and Mociño plants are two collections labelled *Jatropha peltata*; the first of these, no. 4229, seems to have been referred to this species as an afterthought, the authors having previously crossed out the name of another proposed species; the plant is *Manihot foetida*, which does not have peltate leaves; the second collection named *Jatropha peltata* (no. 4231) consists of (1) a fragment of an inflorescence which can be definitely identified as that of *J. podagrica*, since it has the short glabrous calyx and blunt rounded entire discrete lobes of that species, and (2) the major portion of a small and perhaps immature leaf which cannot be identified with certainty but is probably that of *J. platyphylla*; this is indicated by the rather prominent venation and the marginal pubescence characteristic of this species and not of *J. podagrica*, which normally has thick and entirely glabrous blades with slender and rather inconspicuous veins. Sessé and Mociño are known to have collected *J. platyphylla*; a considerable specimen is in the Delessert Herbarium, and is represented in the Field Museum by fragments of leaf and inflorescence and by Field Mus. neg. 24389. If *Jatropha podagrica* was collected by some member of the botanical Expedition, it may well have been in Guatemala, where this species is often cultivated; but if so the above specimen could hardly be the type of *Jatropha peltata* Sessé, for Mociño, the first member of the Expedition to reach Guatemala, did not arrive there until about December 1, 1796, two and one-half years after the publication of *J. peltata*. For this fact I am indebted to Dr. H. W. Rickett.

It would be most unwise to take up the name *Jatropha peltata* for either of the species now well known under other names, in view of the mixture of species included under this name in the Sessé and Mociño collection,

especially since it is probable, but not proven, that the specimen of *Jatropha podagrica* was added to the collection after 1794. It should be noted, however, that *Jatropha peltata* Sessé has priority over *J. peltata* H.B.K. (Nov. Gen. & Sp. 2: 83. 1817), which may therefore be called ***Jatropha Humboldtiana* McVaugh, nom. nov.**

2. *JATROPHA EDULIS* Sessé apud Cerv. l.c.; König, l.c. The original description reads: "*Jatropha* (edulis) floribus caliculatis, folijs cordatis integerimis sublobatisque. Flor. Mex. cum icone." This is clearly the nearly entire-leaved form of *Jatropha Curcas* represented by the Sessé & Mociño specimen (no. 4233). The leaves are almost conventionally cordate and practically unlobed, not at all like the usual form in this species. Essentially the same form was described as *Jatropha yucatanensis* Briq. (Ann. Conserv. Jard. Bot. Génèv. 4: 230. 1900); the type, collected at Campeche by Linden in 1840, is in the Delessert Herbarium and is represented in the Field Museum by fragments of leaf and inflorescence and by Field Mus. neg. 24393.

3. *JATROPHA CILIATA* Sessé apud Cerv. Gaz. Lit. Mex. 3: suppl. 4. 1794; König, l.c.; *J. olivacea* Muell. Arg. Linnaea 34: 207. 1865; *J. grandifrons* L. M. Johnst. Contr. Gray. Herb. 68: 89. 1923. The original description reads: "*Jatropha* (ciliata) floribus caliculatis; foliis cordatis ovatis ciliato denticulatis. Flor. Mex. cum icone." From the description this could hardly be any Mexican species except *J. Alamani* Muell. Arg., *J. olivacea* Muell. Arg., or *J. cordata* (Orteg.) Muell. Arg. Both the first and the last appear to have been known to Sessé and Mociño and presumably to Cervantes under the other names, and the ample flowering and foliage specimens under this name in the herbarium (no. 4226) are unquestionably *J. olivacea*. This species was known to Mueller only through a collection (not seen by me) made by Liebmann at San Juan del Estado, Oaxaca; it has since been recollected at the type-locality (*L. C. Smith* 467, May 6, 1895), and is known from various localities in central Oaxaca and from Río de San Francisco, Puebla (*Purpus* 1050, August 1909) and from the Valley of Mexico (Hill of Ixtapalapa, *Pringle* 6348, June 13, 1896). The number of glandular setae and the amount of toothing and lobing are very variable in this species; some collections (e.g. *Purpus* 1050) have the leaves eglandular and almost unlobed, while others have them copiously glandular-ciliate and conspicuously jagged-lobed. The type of *J. grandifrons* (*Conzatti & Gonzales* 1206, in Herb. Gray ! ) is an average mature specimen of the species. It should be noted that *J. ciliata* Muell. Arg. [Linnaea 34: 209. 1865], a Peruvian species, must take another name because of the earlier *J. ciliata* Sessé. Several names are apparently available, including *J. Augusti* Pax & Hoffm., *J. Hoffmanniae* Croiz. [*J. longipedunculata* Pax & Hoffm.], and *J. Weberbaueri* Pax & Hoffm., but at



the present time it is impossible to ascertain the identities of these species and the points, if any, by which they differ from *J. ciliata* Muell. Arg.; it would be precipitate to rename the latter before thorough investigation of the group.

4. *JATROPHA DIOICA* Sessé apud Cerv. l.c.; König, l.c.; *Mozinna spathulata* Orteg. Dec. Pl. 8: 105. pl. 13. 29 Ja, 1799; *Jatropha spatulata* Muell. Arg.

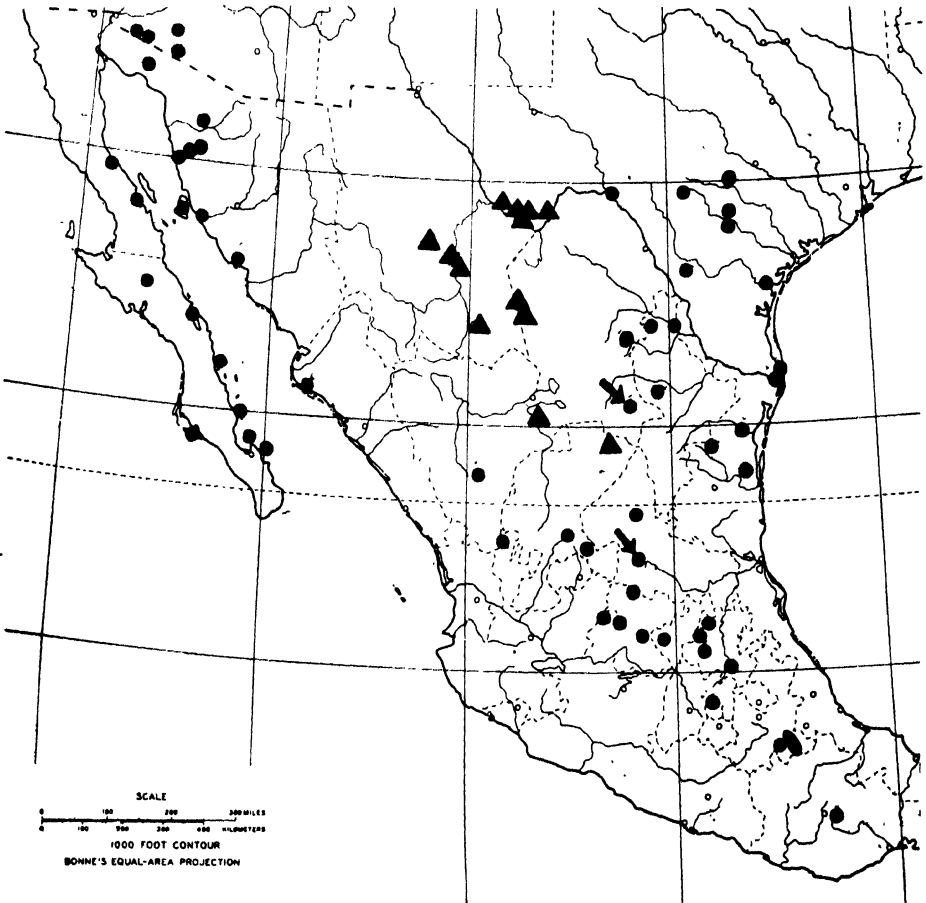


FIG. 1. The distribution of *Jatropha dioica* and allied species. Dots in the Gulf of California region (Sinaloa, Sonora, Baja California and Arizona) show the known occurrences of *J. cuneata* Wiggins & Rollins; dots east and south of this area, *J. dioica* var. *sessiliflora*; triangles, *J. dioica* var. *graminea*; oval, *J. neopanciflora*. The dots indicated by arrows refer to the intermediates (cited in the text) between var. *sessiliflora* and var. *graminea*. So far as known neither *J. cuneata* nor *J. dioica* crosses the Sierra Madre Occidental.

The map is based on specimens in the following herbaria: Arnold Arboretum, Field Museum, Gray Herbarium, New York Botanical Garden, United States National Arboretum, United States National Herbarium.

in DC. Prodr. 15(2) : 1081. 1866. The original description reads: "*Jatropha* (Dioica) floribus caliculatis dioicis, foliis oblongo spatulatis. Flor. Mex. cum icone." From this description, with its references to dioecism and oblong-spatulate leaves, this species may be referred confidently to *J. spathulata* or to *J. neopauciflora* Pax. The latter is known only from a small area near the border between Puebla and Oaxaca, whereas the former is the well-known "Sangre de Drago" (now often "sangregado") of the arid uplands of eastern and southern Mexico; the Sessé and Mocino specimen of *J. dioica* (no. 4238) is an ample (though sterile) one, unquestionably *J. spathulata*.

It is unfortunate that the well-known specific name *spathulata* is to be relegated to synonymy, but the case appears to be sufficiently clear. It should also be emphasized at this time that it seems impossible logically to uphold *Mozinna* as a genus distinct from *Jatropha*. The characters usually relied upon, those of the condensed inflorescence, fascieled cymes and leaves, and reduced number of carpels in *Mozinna*, break down completely when applied in contrast to the same characters in *Jatropha cordata*, *J. cinerea*, *J. cardiophylla* and other Mexican species. The sole remaining character is that of the leaf-shape, which is oblong to spatulate or obovate in *Mozinna* and mostly ovate-cordate in the related species of *Jatropha* proper; this character is scarcely of generic value, particularly as lobed or even cordate leaves appear occasionally in *Mozinna*, especially in very young or vigorous tissues.

*Jatropha dioica* may be readily divided into the following varieties and possibly into others; material is needed, from the region south of Mexico City, to determine the status of plants native to that part of the species' range:

- 1. Leaf blades 2.5-6 times as long as wide, mostly 6-10 mm. wide . . . var. *sessiliflora*
- 1. Leaf-blades 6-17 times as long as wide, mostly 1-4 mm. wide . . . var. *graminea*

4a. *JATROPHA DIOICA* var. **sessiliflora** (Hook.) McVaugh, comb. nov. *Jatropha dioica* Sessé apud Cerv. l.e., as to type. *Mozinna spathulata* Ortega, l.e., as to type. *Loureira cuneifolia* Cav. l.e. 5: 17. pl. 429. [late 1799]. *Mozinna spathulata* var. *sessiliflora* Hook. l.e. 4: pl. 357. 1841. *Jatropha spatulata* var. *genuina* Muell. Arg. in DC. Prodr. 15(2) : 1081. 1866. *Jatropha spatulata* var. *sessiliflora* (Hook.) Muell. Arg. op. cit. 1082. *Zimapania Schiedeana* Engl. & Pax, Natürl. Pflanzenfam. III. 5: 119. f. 75. 1891. *Mozinna sessiliflora* (Hook.) Small, Fl. SE. U. S. 706. 1903.

Leaves oblanceolate to obovate, (2.5) 3.5-5 (7) times as long as wide. Blades mostly 0.6-1 (1.8) cm. wide, 1.5-3.5 (7) cm. long, on shoots exceptionally 3 cm. wide, 4 cm. long, on a petiole 1 cm. long. Width of lobed blades, across the widest points of the lobes, 1.5-3.5 cm., the central lobe then 0.8-1.5 cm. wide.

The TYPE, *Hartweg 37*, from Zacatecas, is evidently an average specimen of this variety, as shown by Hooker's plate 357.

The specimens cited below are from the United States National Herbarium, the Herbarium of the National Arboretum, and the Field Museum; these are indicated by appropriate abbreviations. Where possible the flowering or fruiting condition of the specimen has been indicated also.

*Specimens examined:* TEXAS: Atascosa County: without locality, *Ellen D. Schulz 107*, Apr. 19, 1920 (fl, US). Bexar County: San Antonio, *J. N. Rose 24139*, Oct. 19, 1927 (US). Blanco County: Cañon Blanco, *J. Reverchon 1599*, June, 1875 (fr, US). Cameron County: Brownsville, *R. Runyon 243*, July, 1922 (fl, US). Green Island, *B. C. Tharp*, June 23–29, 1922 (fl, US). Nueces County: Corpus Christi, *A. A. Heller 1550*, Apr. 9–12, 1894 (fl, US), *H. C. Benke 5392*, Apr. 11, 1930 (fl, US). LaSalle County: Cotulla, *Louis Potter*, May 22, 1916 (USNA). Val Verde County: Mouth of the Pecos river, *V. Bailey 275*, May 21, 1900 (fl, US, 2 sheets). County undetermined: South Western Texas, *Ed. Palmer 1234* in 1879–80 (fl & fr, US).

TAMAULIPAS: Near Matamoros, *Berlandier 3210* in 1838 (US); Buena Vista Hacienda, *E. O. Wootton*, June 17, 1919 (US); San Fernando, *J. N. Rose 24323a*, Nov. 2, 1927 (US); Sierra de San Carlos, [Cerro de] la Tamaulipeca, vicinity of San Miguel, *H. H. Bartlett 10544*, *10589*, July 24 and 26, 1930 (both F).

NUEVO LEÓN: Santa Catarina, [near] Monterrey, *Fr. Abbon 91* (Arsène 6244) July, 1911 (US); Lampazos, *Mary T. Edwards 375*, June 26, 1937 (F).

COAHUILA: Monclova, *E. W. Nelson 6747*, May 14, 1902 (US); Saltillo, *Ed. Palmer 226* in 1898 (USNA; some intermediate with var. *graminea*; 1/w about 7/1).

SAN LUIS POTOSÍ: Chareas, *C. L. Lundell 5506*, July–August, 1934 (F); San Luis Potosí market, *Ed. Palmer 612* in 1898 (fr, USNA); San Luis Potosí, *Ed. Palmer 31*, Aug. 18–20, 1902 (US, USNA); Smelter Hill, *C. R. Barnes & W. J. G. Land 106*, Sept. 20, 1908 (fr, F).

ZACATECAS: Pastorilla [i.e. Pastoria ?], *M. E. Jones 425*, May 2, 1892 (US); San Juan Capistrano, *J. N. Rose 3544*, Aug. 21, 1897 (US).

DURANGO: City of Durango, *Ed. Palmer 243*, [June 1–24], 1896 (fl, US).

GUANAJUATO: Empalme de Gonzales, *H. H. Rusby 40*, June, 1910 (US).

QUERÉTARO: Querétaro, *Bro. Agniel 7* (Arsène 10285), 1910–13 (US); *Bro. Agniel s.n.* (Arsène 10449), 1910–13 (fl, US); "Del Ciervo a Sn. Juan," *F. Altamirano 1754*, Aug. 27, 1905 (US).

HIDALGO: Jacala, *F. H. Chase 7336*, July 7, 1939 (F); Ixmiquilpan, *J. N. Rose 8927* in 1905 (US), *L. A. Kenoyer A629*, June 27, 1938 (fl, F); Pachuca, *G. L. Fisher 35499*, July 19, 1935 (fr, F, US); Tula, *Rose 4957*, June 8, 1899 (US).

DISTRITO FEDERAL: Guadalupe, valley of Mexico, *J. N. Rose 8506* in 1905 (US); Mont Zacocalco près Guadalupe, *Bourgeau 184*, June 8, 1865 (fl, US); Guadalupe prope Mexico, *Née* (F).

PUEBLA: See note below.

OAXACA: See note below.

STATE UNDETERMINED: Valley of the Rio Grande below Doñana, *Parry et al.* (Mex. Bound. Surv. 1315) (fl, US); "New Mexico," *C. Wright 1812* in 1851–52 (US); Nova Hispania, *Sessé et al. 4238* ["1944"] in 1787–1804 (F); "*Jatropha dioica* N. ic."); 20 miles south of Nuevo Laredo, *C. H. & M. T. Mueller 446*, July, 1933 (F).

*Note:* *Pringle 9391*, from Tehuacán, Puebla, at 5500 ft., Aug. 7, 1901 (US) differs from var. *sessiliflora* in having the staminate sepals small (0.6–0.7 mm. long and wide), the corolla of 5 free strap-shaped petals 1 mm. wide, 3.5–4 mm. long, the lobes obtuse, not recurved, more or less densely puberulent on both sides, the 9 stamens about 4.5 mm. long, the outer loosely connate 2 mm., the inner connate 3 mm., the anthers 1 mm. long, the leaves up to 3 mm. wide, 21–27 mm. long, on definite petioles 1–1.5 mm. long, the veins reticulate with no evident lateral nerves, the old branches woody, apparently not fleshy, 2.5 mm. in diameter.

*Conzatti (1473) & Vasquez*, from Pueblo Viejo, Dto. Tlaxolula, Oaxaca, at 1750 m., June 19–23, 1906 (US), has leaves up to 15 mm. wide, 30 mm. long, on definite petioles

2 mm. long, all obovate or a little narrower, the veins netted and with several fine lateral pairs, the pistillate sepals linear-elliptic, 1.5-2 mm. wide, 5 mm. long, scarious-margined, rounded at tip, nearly glabrous.

4b. *JATROPHA DIOICA* var. *graminea* McVaugh, var. nov.; folia anguste oblanceolata usque ad linearia, (6) 10-17-plo longiora quam latiora. Limbi plerumque 0.15-0.4 (0.65) cm. lati, 1-4 (8) cm. longi, cum lobati 1-1.5 (rare 4) cm. lati.

TYPE collected at Jimulco, Coahuila, at an elevation of 4200 ft., *Forrest Shreve 9119*, Sept. 14, 1939 (in the Herbarium of the National Arboretum).

*Additional specimens examined*: TEXAS: Brewster County: Boquillas, common, *H. C. Hanson 583*, April 17, 1919 (fl, US); Glenn Springs, *O. E. Sperry 603*, May 3, 1937 (fl, US); Chisos Mts., *C. H. Mueller* (herb. Univ. Tex. 8068), 7/10/31 (fr, US); Lajitas, *E. A. Studhalter 1074*, July, 1925 (fr, US). Presidio County: Presidio, *V. Havard*, Apr. 28, 188- (US).

COAHUILA: Mojada Mts., *M. E. Jones 424*, April 19, 1892 (fl, US); 25 miles west of El Oro, road to Guimbaleté, *S. S. White 2015*, July 24, 1939 (fr, USNA); Jimulco, *C. G. Pringle 155*, Apr. 7 and Aug., 1885 (fl & fr, US); south of Saltillo, *R. Runyon 1330*, July 29, 1929 (US; intermediate with var. sessiliflora; 1/w about 7/1).

CHIHUAHUA: Mecoqui, *Harde LeSueur Mex 10*, August 29-30, 1935 (F); 13 mi. south-east of Saucillo, 4000 ft., *Shreve 8067*, July 29, 1937 (fr, F, US); vicinity of Chihuahua, *Ed. Palmer 125*, Apr. 8-27, 1908 (fl, US); State of Chihuahua [at or near the city of Chihuahua, according to Rose's field-book], *J. N. Rose 4929*, May 11, 1899 (US).

ZACATECAS: Vicinity of Cedros, *J. E. Kirkwood 26*, in 1908 (fr, F); footslopes and their ridges, Cedros, *F. E. Lloyd 146*, Aug., 1908 (fl & fr, US).

SAN LUIS POTOSÍ: Locality unknown, *C. C. Parry & Ed. Palmer 830* in 1878 (fl, US; this approaches var. sessiliflora; 1/w mostly 4-6.5/1).

STATE UNKNOWN: Valley of the Rio Grande below Doñana, *Parry et al.* (Mex. Bound. Surv. 1315a) (fr, US).

5. *JATROPHA PALMATA* Sessé apud Cerv. l.c.; König, l.c. The original description reads: "*Jatropha* (Palmata) Floribus caliculatis, foliis cordatis lobatis denticulato ciliatis. Flor. Mexic." The material under this name in the Sessé and Mocino herbarium (no. 4230) is evidently a species of *Manihot*, with glabrous ovary, glabrous 3- or 5-lobed leaves, the lobes broad, ovate or elliptic, acuminate, entire. The material is too scanty for positive identification, but suggests *M. aesculifolia* (H.B.K.) Pohl. In any event the name cannot be transferred to *Manihot* because of the existence of *M. palmata* (Vell.) Muell. Arg. It should be noted also, however, that the original description of *Jatropha palmata* as given above does not agree with the specimens at hand, or with the characters of *Manihot* in general; "floribus caliculatis" could hardly refer to any *Manihot*, and "foliis . . . denticulato ciliatis" certainly does not refer to the plants under no. 4230. The identity of *Jatropha palmata* cannot be definitely established.

6. *JATROPHA TRILOBA* Sessé apud Cerv. l.c.; König, l.c. The original description reads: "*Jatropha* (triloba) floribus excaliculatis, foliis trilobis acuminatis, integerrimis. Flor. Mex. Hueipochotl Hernandez edit. Roman. 61. Matritens. Tom. 2. p. 361." The plant under this name in the herbarium (no.

4228) is a sterile specimen which agrees exactly in foliar characters with the flowering specimens of *Manihot foetida* comprising no. 4229 and with the plate of *Jatropha triloba* in the Delessert Herbarium (Field Mus. neg. 30857), which seems likewise to represent *M. foetida*, and there seems to be no reason to doubt that *Jatropha triloba* and *Manihot foetida* are identical. The latter species, however, is known only from the original collection, and until it is possible to make an examination of the type it would be precipitate to take up Sessé's name for it, so that I am not transferring it to *Manihot* at this time.

Cervantes' reference to Hernández was evidently ill-founded, for the figure in the 1651 Roman edition of the "Rerum Medicarum" appears to portray *Jatropha gossypifolia*; the calyx and corolla are both clearly shown, as are the numerous flowers and the alternate branching characteristic of the inflorescence of this species; in Hernández' description, moreover, the plant is said to be decumbent or scandent, with scarlet flowers; the principal similarity between *Jatropha triloba* and the plant figured by Hernández is in the leaves, which in both cases have three entire lobes.

7. *JATROPHA QUINQUELOBA* Sessé apud Cerv. l.c.; König, l.c. The description reads: *Jatropha* (Quinqueloba) floribus excaliculatis foliis quinquelobis oblongo ovatis integerrimis. Flora Mex." The herbarium material of this species (no. 4227) appears to agree in every detail with the Sessé & Mociño specimen cited by Mueller Argoviensis as his *Jatropha tubulosa* var. *septemloba* (specimen in the Boissier Herbarium, Field Mus. neg. 24392); the similarity in general characters of leaf and inflorescence is so striking that I should suppose both specimens to have come from the same plant. Mueller's specimen may also be considered as the type-specimen of *J. tubulosa*. He cited no specimens under the inclusive species *tubulosa*, but only under the several varieties: var.  $\alpha$  *septemloba*, var.  $\beta$  *quinqueloba*, var.  $\gamma$  *triloba*. Since Mueller designated no variety *genuina* (as was his usual custom), we may arbitrarily select var. *septemloba*, his first variety, as the most representative of his species; var. *quinqueloba* seems to have been a mixture, perhaps of more than two varieties or species, and var. *triloba* was based on a single specimen, supposedly from Peru where no plants of this affinity are known to occur.

The type-sheet of *J. tubulosa* var. *quinqueloba* (in the Delessert Herbarium, represented by Field Mus. neg. 24391) bears not only the Andrieux specimen cited by Mueller but also a leaf which appears to be that of one of the more densely hairy forms of *J. tubulosa* and which is accompanied by a typical Sessé and Mociño notation: "*Jatropha quinqueloba* N[ueva] E[spaña]." At least two of Mueller's three varieties of *J. tubulosa* are thus based at least in part on material of *J. quinqueloba* Sessé. If the type of var. *septemloba* be regarded as the type of *J. tubulosa* as well, then Mueller's

species is based directly upon *J. quinqueloba*, which is thus the valid name for the plant if it is considered a *Jatropha*. Happily for stability in nomenclature, the name *quinquelobus* is preoccupied in *Cnidoscolus* to which it seems necessary to refer this species; its proper designation here is *Cnidoscolus tubulosus* (Muell. Arg.) Johnston.

8. *JATROPHA OCTANDRA* Sessé apud Cerv. l.c.; König, Tracts Bot. 232. 1805. The description reads: "*Jatropha* (octandra) floribus excaliculatis octandriis, foliis palmatis, lobis intermediis hastatis. Flor. Mex. cum icone." This is apparently a *Cnidoscolus*, but no material of it was found in the herbarium, and its identity is indeterminable from the description alone.

#### SUMMARY

On the basis of specimens in the herbarium of Sessé and Mociño, it is possible to establish the identity of *Jatropha edulis*, *J. ciliata*, *J. dioica*, *J. triloba*, and *J. quinqueloba*, all species described by Sessé in a paper by Cervantes in 1794. The typification of *J. peltata* Sessé and *J. palmata* Sessé is hardly possible on the basis of the material available. The identity of *J. octandra* Sessé, of which no material is available, is unknown. *Jatropha heterophylla* Sessé & Mociño and *J. moluensis* Sessé & Mociño are typified by specimens in the collection.

The following new names are proposed: *Jatropha Humboldtiana*, *J. dioica* var. *sessiliflora*, *J. dioica* var. *graminea*. The following are relegated to synonymy: *Jatropha peltata* H.B.K., *J. edulis* Sessé, *J. yucatanensis* Briq., *J. olivacea* Muell. Arg., *J. grandifrons* Johnst., *J. spathulata* (Orteg.) Muell. Arg., *J. quinqueloba* Sessé.

DIVISION OF PLANT EXPLORATION AND INTRODUCTION,

BUREAU OF PLANT INDUSTRY STATION

BELTSVILLE, MARYLAND

# JUNIPERUS VIRGINIANA, J. HORIZONTALIS, AND J. SCOPULORUM—III. POSSIBLE HYBRIDIZATION OF J. HORIZONTALIS AND J. SCOPULORUM

NORMAN C. FASSETT

Of the several differences between *Juniperus horizontalis* and *J. scopulorum*,<sup>1</sup> four have been chosen as most conveniently dealt with. Table 1 shows a survey of a mass collection from Bridger, Montana, where each individual is erect, with a foliar gland exceeding in length the distance from the gland to the tip of the leaf, with obtuse leaf tips, and with 11-60 per cent of the fruiting peduncles hooked; in other collections of this species they run from 8-70 per cent hooked. Table 2 shows a similar survey of a mass collection of *J. horizontalis*, from a locality about 100 miles to the east of that represented in table 1, on the other side of the Big Horn Mountains. In this collection, every individual is creeping, with foliar gland shorter than the distance from the gland to the tip of the leaf, the leaf tips are apiculate, and 75-100 per cent of the fruiting peduncles are hooked; this last figure may run as low as 70 per cent in other collections. Just across the road from the colony of *J. horizontalis* treated in table 2, is a patch of cedars, obviously *J. scopulorum*. When analyzed, however, they show (table 3) certain tendencies in the direction of the neighboring species, for the foliar gland is sometimes shorter than the distance to the leaf tip, the leaf tips are sometimes acute or even slightly apiculate, and the percentage of hooked peduncles runs higher than is normal for *J. scopulorum*. It appears, then, that in this case *J. horizontalis* is showing some influence on *J. scopulorum*, but *J. scopulorum* is showing no influence on *J. horizontalis*.

TABLE 1. Ten individuals of *J. scopulorum* from Bridger, Montana

Habit	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles curved
Erect	Longer	Obtuse	...
Erect	Longer	Obtuse	19
Erect	Longer	Obtuse	11
Erect	Longer	Obtuse	11
Erect	Longer	Obtuse	...
Erect	Longer	Obtuse	...
Erect	Longer	Obtuse	60
Erect	Longer	Obtuse	47
Erect	Longer	Obtuse	...
Erect	Longer	Obtuse	33

<sup>1</sup> Bull. Torrey Club 71: 410-418, 1944.

TABLE 2. *Nine individuals of J. horizontalis from 5 miles north of Sheridan, Wyoming*

Habit	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles curved
Creeping	Shorter	Apiculate	.....
Creeping	Shorter	Apiculate	100
Creeping	Shorter	Apiculate	100
Creeping	Shorter	Apiculate	100
Creeping	Shorter	Apiculate	75
Creeping	Shorter	Apiculate	.....
Creeping	Shorter	Apiculate	.....
Creeping	Shorter	Apiculate	.....
Creeping	Shorter	Apiculate	88

About 20 miles west of this point, near Steamboat Rock on the east slope of the Big Horn Mountains, six individuals of *J. horizontalis* were found; they, likewise, showed no characters suggesting influence of *J. scopulorum*.

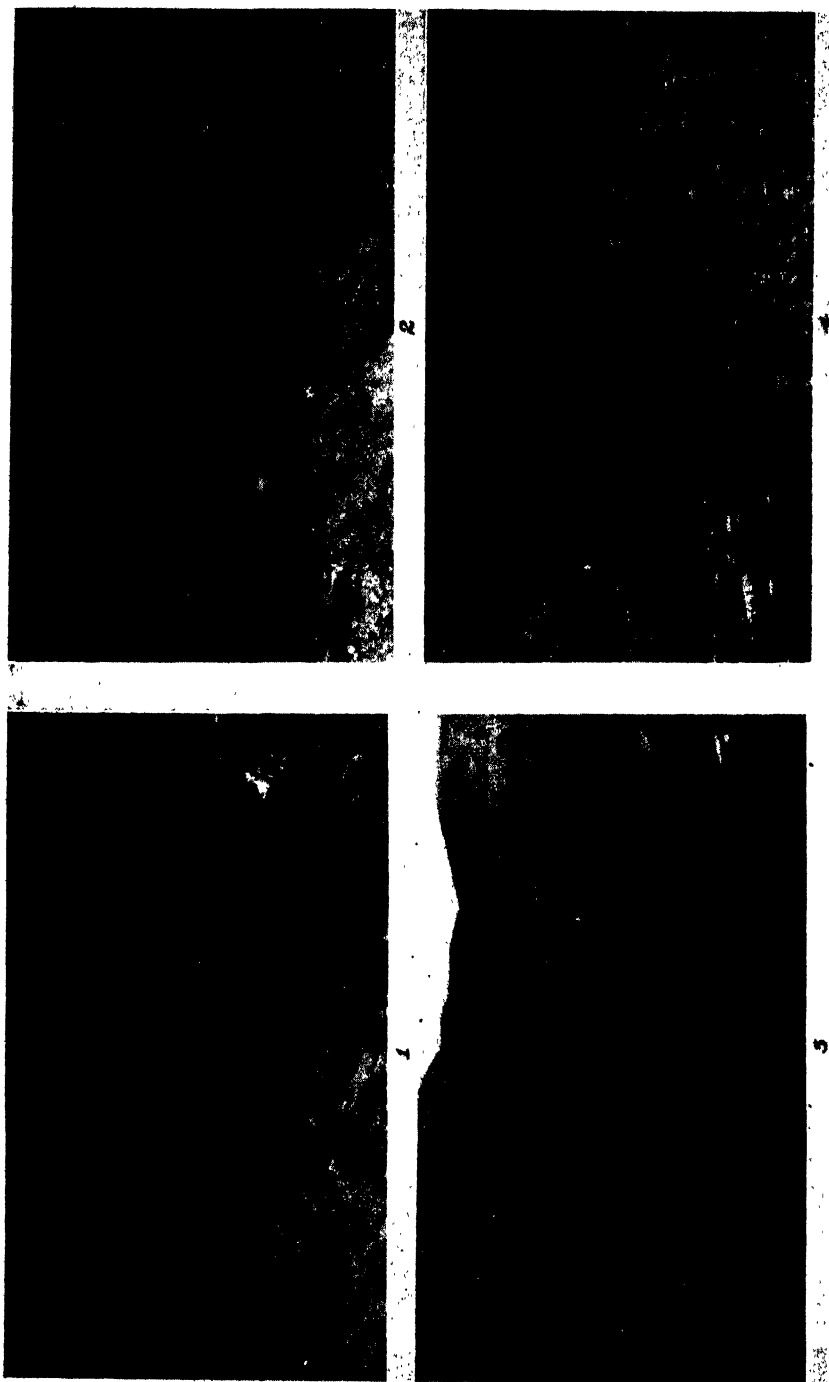
The west slopes of the Big Horn Mountains are covered with great masses of red cedar (figs. 1-2), and these extend westward over the plains for about ten miles from the foot of the mountains (figs. 3-4). Many of the plants are erect and seem to be good *J. scopulorum* except for the slightly high proportion of hooked peduncles (table 4), while other plants are depressed, with about the general habit of the eastern *J. communis* var. *depressa*. In some cases, both types appear together (table 4; fig. 3), while in others the depressed form alone occurs (table 5).

No *J. horizontalis* was observed in the region; that the depressed habit of the *J. scopulorum* is due to hybridization with that species is highly conjectural. It must be noted that the populations on the west slopes of the Big Horns and on the adjacent plains consist of two relatively constant types,

TABLE 3. *Ten individuals of a hybrid swarm of J. scopulorum and J. horizontalis from 5 miles north of Sheridan, Wyoming*

Habit	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles curved
Erect	Shorter	Obtuse	92
Erect	Shorter	Obtuse	.....
Erect	Longer	Obtuse	74
Erect	Both	Obtuse	75
Erect	Both	Acute	56
Erect	Longer	Obtuse	78
Erect	Longer	Obtuse	72
Erect	Longer	Obtuse	76
Erect	Shorter	Obtuse but minutely apiculate	.....
Erect	Longer	Obtuse	.....





FIGS. 1, 2. *Juniperus scopulorum* var. *patens* on the west slopes of the Big Horn Mountains, along highway Wyoming 14, near the western edge of Big Horn National Forest. FIG. 3. *J. scopulorum* (left) and *J. scopulorum* var. *patens* (right) on plains west of Big Horn Mountains. FIG. 4. *J. scopulorum* var. *patens* on plains west of Big Horn Mountains.

TABLE 4. *Fourteen individuals of J. scopulorum and J. scopulorum var. patens from the plains between the Big Horn River and the Big Horn Mountains, east of Lovell, Wyoming*

Habit	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles hooked
Depressed	Longer	Obtuse	72
Depressed	Longer	Obtuse	72
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	.....
Depressed	Shorter	Acute	.....
(Semijuvenile foliage)			
Erect	Longer	Obtuse	91
Erect	Longer	Obtuse	..
Erect	Longer	Obtuse	38
Erect	Longer	Obtuse	..

differing only in habit. This is in marked contrast to the purported hybrid colony represented by table 3, where three of the characters of *J. horizontalis* had more or less infiltrated a colony of *J. scopulorum*, and in extreme contrast to the hybrid colonies<sup>2</sup> of *J. virginiana* and *J. scopulorum*, which showed a multitude of recombinations of the characters of the two parent species.

If these depressed individuals of *J. scopulorum* are actually the product of a cross with *J. horizontalis*, they are not the result of any recent hybridization, but rather of some ancient gene flow from one species into the other. In any case, it is a fact that such individuals are characteristic of certain

TABLE 5. *Twelve individuals of J. scopulorum var. patens from the west slope of Big Horn Mountains, east of Lovell, Wyoming*

Habit	Gland shorter than distance to tip of leaf, or longer	Leaf tips	Per cent of peduncles hooked
Depressed	Longer	Obtuse	48
Depressed	Longer	Obtuse	..
Depressed	Longer	Obtuse	50
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	53
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	74
Depressed	Longer	Obtuse	70
Depressed	Longer	Obtuse	.....
Depressed	Longer	Obtuse	.....
Depressed	Longer	Subacute	50
Depressed	Longer	Obtuse	57

<sup>2</sup> Bull. Torrey Club 71: 475-483. 1944.

localities within the range of *J. scopulorum*. This phase of the species may, for convenience, be called:

*J. scopulorum* Sarg. var. *patens* Fassett, var. nov. Plantae circa 1 m. altae, patentes. WYOMING: between the Big Horn River and the Big Horn Mountains, east of Lovell, June 24, 1941, *N. C. Fassett 22062* (TYPE in Herb. Univ. of Wis.) ; west slope of Big Horn Mountains near Lovell, June 24, 1941, *Fassett*, many numbers. The following collections are in the Arnold Arboretum. WYOMING: Big Horn Mts., 6400 ft. alt., on road Sheridan to Dome Lake, Sept. 1, 1900, *J. G. Jack* [foliage of *J. scopulorum*, but labelled "*Juniperus Sabina, procumbens*"]. ALBERTA: Devil's Head Lake, Lat. 51° 15', Long. 115° 25', Banff, July 6, 1891, *Macoun* [foliage of *J. scopulorum*, but labelled "*Juniperus Sabina* var. *procumbens*"]; dry slopes, Banff, Aug. 9, 1904, *Alfred Rehder*, "spreading shrub,  $\frac{1}{2}$ –1 m.; foliage yellowish green"; same data but "foliage bluish green"; Banff, August 9, 1897, *C. S. Sargent*, "small plant, rare."

The advisability of naming hybrids has recently been discussed by Camp & Gilly;<sup>3</sup> the case of *J. virginiana* and *J. scopulorum*<sup>4</sup> is like that of *Vaccinium atrococcum* and *V. Torreyanum*, with a heterozygous population in which it is not practicable to apply names to the various elements, while the hybrids of *J. scopulorum* and *J. horizontalis* (if indeed they are hybrids of those species) appear as a more homogeneous population of decumbent shrubs with the foliage identical with or similar to that of *J. scopulorum*, and only occasionally approaching that of *J. horizontalis*.

The writer is indebted to the Wisconsin Alumni Research Foundation for travel funds to study these plants in Wyoming, and to the curators of the Gray Herbarium and of the Arnold Arboretum for loans of herbarium material.

#### SUMMARY

When *Juniperus scopulorum* and *J. horizontalis* occur together, there are several things that may happen. Near Sheridan, Wyoming, the two species occur on opposite sides of a road; *J. scopulorum* shows tendencies toward *J. horizontalis* in several characters, but *J. horizontalis* shows no characters of *J. scopulorum*. On the west slopes of the Big Horn Mountains, Wyoming, and on the adjacent plains, where no *J. horizontalis* was observed, and in the vicinity of Banff, Alberta, where the writer has not had opportunity to make field studies, occurs a depressed shrub with the foliage and fruit of *J. scopulorum*, which is described as *J. scopulorum* var. *patens*, var. nov.; it is suggested that this variety may have arisen by some ancient hybridization of *J. scopulorum* with *J. horizontalis*.

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<sup>3</sup> *Brittonia* 4: 362–363. 1943.

<sup>4</sup> *Bull. Torrey Club* 71: 475–488. 1944.

# RHIZIDIOMYCES HIRSUTUS SP. NOV., A HAIRY ANISOCHYTRID FROM BRAZIL

JOHN S. KARLING

Anisochytrids are simple fungi with anteriorly uniflagellate zoospores, which resemble the true chytrids in structure and development, but because of the anterior position of the flagellum on the zoospores they have been separated from the Chytridiales and segregated by the author<sup>1</sup> in another order, the Anisochytridales. They are comparatively few in number as far as is now known and up to the present time less than a score of species have been recorded in mycological literature.

In a previous publication relating to aquatic fungi of the Amazon Valley in Brazil the author<sup>2</sup> reported the occurrence of two known anisochytrids, *R. apophysatus* and *R. bivellatus*, in South America and described a third species, *R. Hansonae*, which was isolated from moist soil samples collected at San Carlos, Matto Grosso and in Manaus, Amazonas. Since that time a fourth species of the same genus has been found in moist leaf mold<sup>3</sup> from Seringal Monte Alegre about sixty miles southeast of Rio Branco in Acre Territory. This species differs primarily from the known members of *Rhizidiomyces* by the presence of numerous elongate coarse hairs on the surface of the sporangia. Otherwise, it is non-apophysate and saprophytic like *R. bivellatus* and *R. Hansonae*, with large zoospores of about the same size as those of *R. bivellatus*. The hirsute character of the sporangia, however, clearly distinguishes this Brazilian fungus from the other species of *Rhizidiomyces*, and it is accordingly regarded by the writer as a new species for which the name *R. hirsutus* is proposed.

**Rhizidiomyces hirsutus** Karling, sp. nov. Sporangii extramatrixlibus, non apophysatis, hyalinis, globosis (6-180  $\mu$  diam.), ovalibus (8-20  $\times$  20-60  $\mu$ ), pyriformibus, obpyriformibus, oblongis, aut irregularibus, 3-47 setis elongatis crassis (15-190  $\mu$  longis, 2-3  $\mu$  latis) munitis. Zoosporis ovalibus, oblongis, aut elongatis, 3-4  $\times$  6-8  $\mu$ , unam pluresve granulas minutas refringentes habentibus; flagello 14-18  $\mu$  longo. Systemate rhizoideo valde ramoso, pro more monoaxiali, e basi sporangii orto thallo in substrato solido crescenti, saepe e locis pluribus orto et visu leviter radiali thallo in media liquida crescenti.

<sup>1</sup> Karling, J. S. 1943. The life history of *Anisoldipidium Ectocarpus* gen. nov. et. sp. nov., and a synopsis and classification of other fungi with anteriorly uniflagellate zoospores. Am. Jour. Bot. 30: 637-648.

<sup>2</sup> ———. 1944. Brazilian anisochytrids. Ibid 31: 391-397.

<sup>3</sup> The writer is grateful to Dr. J. T. Baldwin for collecting the leaf mold on one of his trips to the Acre Territory.

Saprophytic in moist leaf mold, Seringal Monte Alegre, Acre Territory, Brazil.

This species was first isolated on bits of hemp seed, but has since been grown successfully on bits of corn and grass leaves, onion skin, insect exuviae, chitin, pollen grains of numerous Angiosperms, synthetic agar media and in liquid media. However, the best and most abundant growth occurs on hemp seed where the sporangia and surface hairs attain their greatest diameter and length. When grown on this substratum, the young and mature sporangia are usually filled with refractive bodies of various sizes (figs. 15-17) which may be so numerous and closely crowded that they often become angular in shape. Occasionally, the refractive bodies may even occur in the rhizoids and sporangial hairs (figs. 17, 18). These refringent bodies are blackened by osmic acid, indicating that they are of an oily composition.

Although *R. hirsutus* grows readily as a saprophyte on various substrata and synthetic media, it may occasionally infect the oogonia of *Achlya flagellata* when the two fungi are grown together on hemp seeds. In such cases the sporangia of the parasite resemble somewhat those of *R. apophysatus* which may also be spiny, according to Zopf,<sup>4</sup> and infect the same host. However, the length and coarseness of the hairs on the sporangia as well as the large zoospores produced by *R. hirsutus* distinguish it quite clearly from this species.

The usual method of development of *R. hirsutus* is so similar to that of *R. bivellatus* and *R. Hansonii* that it is not necessary to describe it in detail. The present description will accordingly be limited largely to differences and variations of this process. However, it may be noted first that in the normal developmental cycle, the zoospores (figs. 2, 3), which usually contain one fairly large and several smaller granules, come to rest (fig. 4) and develop one or more germ tubes which penetrate the substratum (fig. 5). Shortly after this has occurred, small buds appear on the surface of the spore and elongate into filaments (fig. 15) and later become the sporangial hairs. The germ tube branches and gradually develops into the rhizoidal system (fig. 16), while the extramatrical spore body enlarges and becomes the sporangium. At maturity the thallus of *R. hirsutus* has the structure and appearance shown in figure 1. The exit tube then begins to develop as a broad, more or less hyaline papilla (fig. 1) and elongates to from 8 to 60  $\mu$  as the sporeplasm slowly moves upward. As this upward flow of protoplasm continues, the tube expands at the tip (fig. 12), and finally the entire content of the sporangium passes out and undergoes cleavage into zoospores (figs. 13, 14). As in other species of *Rhizidiomyces* described by the author, the

<sup>4</sup> Zopf, W. 1884. Zur Kenntniss der Phycomyeten. Nova Acta Leop.-Carol. Akad. 47: 188.

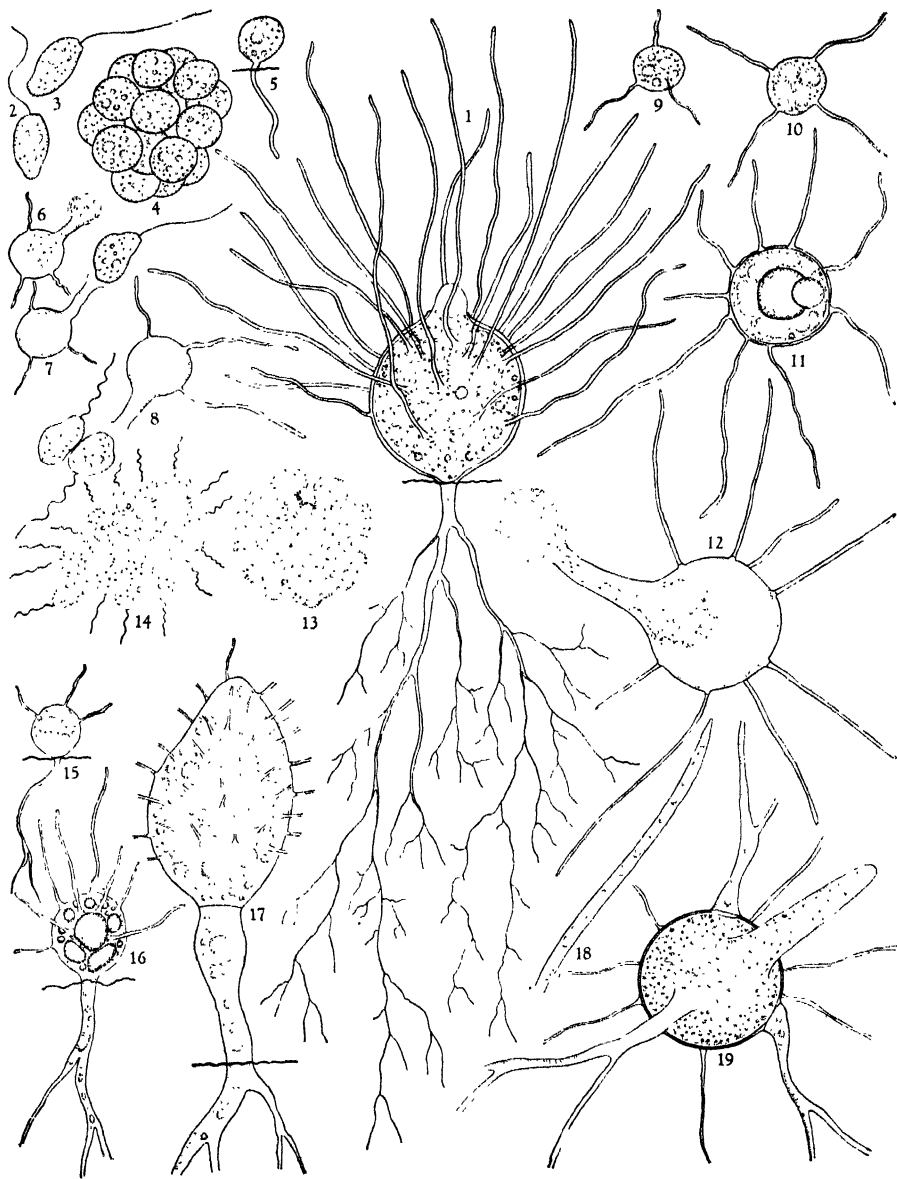


FIG. 1. Mature thallus of *R. hirsutus*.  $\times 600$ . FIGS. 2, 3. Zoospores with one fairly large and several minute granules.  $\times 1000$ . FIG. 4. Mass of quiescent spores.  $\times 1000$ . FIG. 5. Germination of spore on a solid substratum.  $\times 1000$ . FIG. 6. Emergence of the protoplasm of a spore or minute sporangium with three short setae.  $\times 1200$ . FIG. 7. Later stage showing protoplasm transformed into a zoospore.  $\times 1200$ . FIG. 8. Slightly larger sporangium which has formed two zoospores.  $\times 1200$ . FIGS. 9, 10, 11. Stages in the development of extramatrical thalli growing in a liquid medium; peripheral hairs functioning as rhizoids.  $\times 1000$ . FIG. 12. Emergence of protoplasm.  $\times 1000$ . FIGS. 13, 14. Cleavage of protoplasm into zoospores.  $\times 800$ . FIGS. 15, 16. Successive stages of thallus development on a solid substratum.  $\times 1000$ . FIG. 17. Sporangium with broken hairs.  $\times 1000$ . FIG. 18. Enlarged portion of a sporangial hair containing numerous refractive bodies.  $\times 1800$ . FIG. 19. Extramatrical thallus with rhizoids and sporangial hairs.  $\times 1000$ .

emerged protoplasmic mass appears to be naked, and no vesicular membrane has been observed around the zoospores.

As was noted earlier, the sporangial hairs begin as small buds on the surface of the enlarging spore body, and in the early stages they are almost indistinguishable from germ tubes except for their smaller diameter. On large mature sporangia they may become  $190\ \mu$  long and from 2 to  $3\ \mu$  in diameter. As far as present observations go, the hairs rarely branch, but they often contain several rod-shaped, oval, and globular refractive bodies (fig. 18). In contaminated hemp seed and other cultures, numerous protozoa, rotifers and other microscopic animals are often present, and these may crawl and feed back and forth over the sporangia. In such cases the sporangial hairs often break off and leave short stubs on the surface of the sporangia, as shown in figure 17.

Numerous variations and abnormalities of the above described developmental cycle occur. Quite often the zoospores fail to become actively motile and round up after a brief period of rocking movement. As a consequence, loose masses of quiescent spores frequently occur (fig. 3) which resemble the cystospores of higher Phycomycetes. These spores may disintegrate or germinate directly in water without coming into contact with a solid substratum. In a few cases observed, such spores developed short hairs and an exit tube and formed a zoospore without further growth. Figure 6 shows a spore or minute sporangium the content of which is emerging through a short exit tube. The discharged protoplasm then developed without cleavage into a normal-sized zoospore (fig. 7), which became flagellate and swam away. The emergence of protoplasm from such spores and its transformation into zoospores do not differ fundamentally from the changes involved in diplanetism in higher Phycomycetes. A slightly larger spore or sporangium is shown in figure 8, from which the content has emerged and divided into two normal zoospores.

In synthetic liquid media the spores may form hairs and develop into fairly large thalli without forming rhizoids (figs. 9-12). In such thalli the tenuous hairs apparently function as absorbing organs and take the place of rhizoids in this physiological function, because the incipient sporangia grow in size, mature, and form zoospores in the normal manner (figs. 12-14). From other completely extramatrical thalli, definite rhizoids may develop in addition to sporangial hairs (fig. 19). The rhizoids of these thalli often arise at several points on the surface of the sporangium, branch freely, and extend somewhat radially in the surrounding liquid medium. Except for their hyaline color, such thalli resemble the extramatrical polyrhizoidal ones described by the author in *R. bivellatus*.

In large abnormal sporangia the exit tube may attain a length of  $170\ \mu$  and branch one or several times. In such cases, the protoplasm is often used

up in exit-tube development and becomes so dispersed that no zoospores are produced. Abnormal sporangia with as many as from two to four exit tubes may also occur in *R. hirsutus*. Sometimes the protoplasm fails to emerge through the exit tube, with the result that cleavage and development of zoospores may occur within the sporangium. Such zoospores, however, do not usually become motile. In other cases observed, part of the protoplasmic mass remained in the sporangium and underwent cleavage into zoospores which became motile and later escaped singly through the exit tube. Occasionally, cleavage may be incomplete or unequal so that large bi-, tri-, and tetra-flagellate zoospores are formed.

So far no resting spores or dormant thick-walled sporangia have been found, and it is not known by what means *R. hirsutus* is able to survive unfavorable environmental conditions.

#### SUMMARY

*Rhizidiomyces hirsutus* sp. nov. was isolated on hemp seed from moist leaf mold collected at Seringal Monte Alegre in Acre Territory, Brazil. It grows well as a saprophyte on various solid vegetable and animal substrata, synthetic agar, and in synthetic liquid media, but may occasionally parasitize the oogonia of *Achlya flagellata* when grown together with this fungus on hemp seed. It differs primarily from other species of *Rhizidiomyces* by the presence of numerous long coarse hairs on the surface of the sporangia and by the production of large zoospores. No resting spores or dormant sporangia have been found.

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HISTORY AND NOMENCLATURE OF THE HIGHER UNITS  
OF CLASSIFICATION

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Immediate taxonomic needs have repeatedly forced me to consult the prefaces of the works of Linnaeus, Adanson, Haller, Necker, Ventenat, Lamarek, A. L. de Jussieu, Jaume-St. Hilaire, A. de Jussieu, Robert Brown, Lindley, and other less well-known botanists. As a byproduct of these consultations I have collected certain notes which are interesting for the history of botanical thought in general, and even more valuable, I believe, as an elucidation of much that is obscure about the origin and nature of systematic units above the genus. To be informed about history may rate as an amenity, but to handle these units with purposeful understanding is a necessity. How little we know about them is revealed by a glance through the pages of so widely consulted a reference as the *Natürlichen Pflanzenfamilien*, 2nd edition. In one volume (op. cit. 21. 1925) Gilg, Pilger, and Melchior follow different standards in presenting the synonymy of the Ochnaceae, Caryocaraceae, and Violaceae, only that the last family being so some extent satisfactory.

This study must be brief; it acquaints the reader with certain works which it proves essential to appraise and to know, but makes no claim to being exhaustive. The student of any form of thought reckons with the fact that thought does not form itself of a sudden, but many are the rivulets which build the head of the stream. No doubt, the inception of true, or natural classification may be carried back at least to the days of Caesalpin. To delve that far back, and to check each strand to its prime source, is definitely not the purpose of this study. To fulfill its aims, I believe, this study needs but to consider the lapse of a century, between 1735 and 1835. Within these hundred years natural classification was born, brought to flower, and mostly elaborated in the nomenclatural sense.

## DESCRIPTION VS. INTERPRETATION

Hardly anything can be understood unless its inmost parts are digested and brought forth in as simple a manner as possible. Nature is full of facts, and history is bespangled with dates, but merely to record them serves little purpose. To grasp the subject with which we are about to deal, let us suppose that, clad in pelts and brought back to an untutored age, we face the world of vegetables. Some plants we can use, others we cannot. Some give health, others destroy it. Almost of necessity, our first classification will tend to divide the plants around us into the useful and the noxious. Later on,

having mastered writing, we will make certain that our descendants shall profit from our knowledge by *describing* these plants under chapters such as "Plants with roots that can be eaten," "Herbs which are good in love-potions and magic brews," and the like. We may, of course, take into account the fact that some of these plants are tree-like and perennial, others fugacious weeds.

As time wears off, and our grasp of nature becomes more self-conscious and firmer, we will give ourselves some account of the fact that certain groups, like the leguminous, characterized by common kinship, may well happen to include trees, shrubs, and herbs, and be useful or not for immediate material needs. By investigating these groups as something somehow related, we shall perceive that, while they may be much alike in fruit, they may differ in flower and foliage, or the other way around. Almost unconsciously, we shall be drawn to use these characters in order to arrange the plants which we describe within certain groups, clans, or tribes. By so doing we will implement our descriptions with *artificial keys*. If, mistaking these keys as true classification, we rely on the compound nature of the foliage to associate *Gymnocladus* with *Cladrastis*, excluding *Cercis*; on the papilionaceous corolla to place together *Cladrastis* and *Cercis*, ruling out *Gymnocladus*; on the male ament to set up as one unit *Populus*, *Salix*, *Carpinus*, *Corylus*, *Quercus*, *Juglans*, *Carya*, and *Myrica*; we shall write an *artificial classification*.

As a final stage in our botanical toils, and with the world as our province, we shall realize that no amount of laborious describing or keying avails us to put together *Hura crepitans* and *Euphorbia obesa*, for these plants are altogether unlike in body, fruit, and flower. After much thought, and through a careful study of true relationships, we shall soar to the perception of a quivering, evolutionary knot of life which binds *Hura* and *Euphorbia*. This knot we shall refer to as the Euphorbiaceae; we shall feel competent to describe its characters, more or less adequately—for indeed there are none—only after we shall have thought ourselves out. At this stage we shall have reached a *natural classification*.

Since human thought runs in channels, although some men are far in advance of others, it is not to be expected that rudimentary botany, artificial botany, and natural botany have parted company of a sudden. Transitional stages have connected these three brands of botany, the conservative and the unimaginative being forever fated to fight against the progressive and the imaginative.

It will readily be seen that great historical significance attaches to a work, regardless of its length or acknowledged purpose, in which an author begins to give himself *conscious account* of new facts and needs, and begins to act *deliberately* in order to meet them. The precursor, whose thought is

not always conscious, and whose actions are not necessarily deliberate, may thus happen to yield in the estimation of mankind to the vulgarizer, who is able to pass new ideas on to others ready for elaboration and immediate use. Service, obviously, is the earmark of true genius.

This study is not concerned with the transitional stage<sup>1</sup> which has connected rudimentary botany with artificial botany, but only with certain steps that have connected artificial classification with natural classification. These crucial steps have been taken by comparatively few authors, often in short pages. He who clearly began to see that puttering with certain characters of the corolla and of the stamens could yield only endless schemes of artificial classification, that is, nothing better than artificial keys, and to understand that artificial keys are not true botany, is to our science what the discoverer of the symbol zero is to mathematics. Once we know these creative souls, and have their statements before our eyes, we are provided with a safe yardstick to measure progress, and to judge of services rendered. We can readily weigh Adanson's work against Necker's, despite superficial resemblances which may induce some to dismiss both these men as crackpots. The pedagogical value attaching to the possession of such a yardstick will be apparent to an imaginative teacher, whose problem is to quicken the best in the minds of youth.

#### LINNAEUS, ADANSON, HALLER, AND GLEDITSCH

In 1735 a thin folio came out of the press in which a young man, known to us as Linnaeus, set forth certain generalities about the three classic kingdoms of nature. In this work, the *Systema Naturae*, Linnaeus introduced a schematic arrangement of the world of vegetables with some plain figures. This arrangement is titled "Clavis Systematis Sexualis," and begins: "Nuptiae Plantarum. Actus generationis incolarum Regni Vegetabilis, *Florescentia*." This is followed, wholly in the manner of a modern taxonomic key, by two divisions, reading: "Publicae. Nuptiae coram totum mundum

<sup>1</sup> Rudimentary botany held its own to within half a century before the beginnings of natural classification. Ray's *Methodus Plantarum* (1682), though enriched by remarkable studies on the structure of the seed, is still remote from anything heralding the new era, and, as Ray himself admits (*Meth. Pl. Emend. Dedicatio* [3] 1703), was held in contempt by contemporary botanists. It is difficult indeed to believe that groups formed by *Ulmus*, *Fraxinus*, *Acer*, *Carpinus*, and *Tilia*, or by *Chelidonium*, *Ranunculus*, *Malva*, and *Fragaria* can be the modern Orders as suggested by the most recent bibliographer of Ray (Raven, *John Ray Naturalist, His Life Works*, 194. 1942). The speed at which botany could progress at this period, however, is nowhere better documented than in Ray's *Methodus Plantarum Emendata* (1703). This work bears witness to his greatness as a progressive thinker. Aside from its introduction of the Monocotyledons and Dicotyledons, its contributions to nomenclature, and its excellent discussion of generalities, Ray's second *Methodus* may easily lay claim to have begun classification by families in its treatment of the liliaceous and graminaceous alliances. Ray holds a position of preëminence among the forerunners of natural classification, and ranks very high among botanists and naturalists of creative ability.

visibilem aperte celebrantur. *Flores unicuique visibiles sunt*," "Clandestinae. Nuptiae clam instituuntur. *Flores oculis nostris nudis vix conspiciuntur*. CRYPTOGAMIA." The "Nuptiae Publicae," which Linnaeus by an oversight failed to designate as PHANEROGAMIA, are once more broken down into two, as follows: "Monoclinia. Mariti & Uxores uno eodemque Thalamo gaudent. *Flores omnes hermaphroditi sunt, & stamina cum pistillis in eodem flore*," "Dielinia. a *δῖς* bis & *κλινῇ* Lectus, Thalamus. Mariti seu feminae distinctis thalamis gaudent, *Flores masculini vel feminini in eadem specie*."

Thus robustly begun, this key continues in the same vein assimilating the stamens to husbands and the pistils to wives, until "Syngenesia" is reached, in which "Mariti cum genitalibus foedus constituerunt," and "Polyandria" briefly described as a condition under which "Mariti viginta & ultra in eodem cum femina thalamo."

That such a key as this had an instantaneous and enormous appeal to the mind of the public can readily be understood. By a bold stroke of the pen the nebulous world of plants was made to act like husbands and wives in unconcerned freedom, and everybody prepared to grasp the meaning of Monoecia and Dioecia, Syngenesia and Polygamia without effort. The educational value of this key, scientifically speaking, was tremendous, for it dispensed with musty tomes, learned verbiage, pompous trappings, and the like, to appeal directly to the flowers of the field. Very few works may compete with the *Systema Naturae* in purposefulness and power of well-meant vulgarization.

The boldness of the Linnean stroke raised in some quarters an outcry that this wild man was a crackpot. Siegesbeck, for instance, who could not see that the genius and the crackpot can look alike, but only the former yields true service, came forward with an account of "Botanosophiae verioris," dignified and orthodox botany, as we might say, in which he proclaimed that God could not permit, even among plants, "Such odious vice as that several males (anthers) should possess one wife (pistil) in common, or that a true husband should, in certain composite flowers, besides its legitimate partner, have near it illegitimate mistresses" (B. D. Jackson, *Linnaeus*, 170. 1923).

At this late hour, we are fortunately free from the necessity of sitting as judge on the petty morals of the case, and quite aware that Linnaeus' thunderbolt aroused a niggardly world to pay salaries even to some in the Siegesbeckian tradition. The question which is relevant to us is: Did Linnaeus thoroughly accept the Sexual System? The apparent answer should be yes, for this System is associated with his name wherever botany is taught, and is definitely used in the Linnean works. The System is glaringly artificial, for it associates, for instance, *Asarum*, *Portulaca*, and *Triumfetta* in one group. If Linnaeus accepted it without qualification, he is not to be rated

as a modern botanist, despite his having given us the binomial system of nomenclature.

The years spent by Linnaeus in western Europe (April 1735 to June 1738) are crucial for botany. Linnaeus published in this period much which he had prepared, if not actually written, during his years as an impecunious and often harassed student at the University of Uppsala. Nothing, however, is immature or half-baked in these works; Linnaeus comes out of their pages like Minerva out of the brains of Jupiter, armed and clad from head to foot. Unknown as they are today to the botanical majority, these works rank as Linnaeus's very best, and whatever he later achieved, when possessed of vastly greater means, can be traced directly to them.

Here are some of the thoughts of Linnaeus, clearly expressed in the three years which followed the publication of the *Systema Naturae* in 1735:

(a) Nothing can be understood without a clear method by which things like and unlike can be set apart. Our concepts are bound to be much clearer if we use as natural a method as possible. A natural method is all the more necessary, and all the more hard to write, as we face a greater number of subjects. Since by the Creator's fiat the world of plants is all-pervading, it is in botany that a natural method has the best chance of being ultimately worked out. Only through this method may we hope to gain a lucid perception of plant-life.<sup>2</sup>

(b) Many are preyed upon by an almost morbid fear of using some method of classification to which they are not accustomed. Some would rather read the most elementary primer than to consult a work which does not suit their notions. Since it is probable that most botanists establish their preferences in their early years, the students should be accustomed to use all kinds of methods, thereby freeing their minds from pettiness. Even a student is qualified to work out a system of his own if he does not find what he looks for in the current systems. For the same genera are not known to every botanist.<sup>3</sup>

The texts quoted are a sample of the Linnean thought, and could be freely implemented if space did not forbid. To comment on them is superfluous. Linnaeus definitely knew that classification is ultimately bound to rest

<sup>2</sup> *Genera Plantarum*, Ratio Operis. No. 1. 1737. "Omnia, quae a nobis vere dignosci possunt, dependent a clara Methodo, qua distinguimus similia a dissimilibus. Haec Methodus quo magis naturales comprehendit distinctiones, eo clarior rerum nobis nascitur idaea. Quo circa plures versatur noster conceptus objecta, eo difficilius elaboratur methodus, ac magis necessaria evadit. Nullibi tot objecta humanis sensibus obiectit Summus Conditor, ac in Regno Vegetabili, quod totum istum, quem inhabitamus, globum tegit, replet. Ergo si ullibi pura methodus e re est, sane hic; si Vegetabilium claram idaeam obtinere sperabimus."

<sup>3</sup> *Classes Plantarum*, Praefatio. 1738 "Nescio quid fascinat homines, ut non possint alteram methodum videre absque perturbatione; potius legunt libellum secundum A.B.C. scriptum, quam secundum notas aliquas plantae; credo vix aliud, quam Botanici ad unam methodum dispositus a teneris animus; optandum itaque foret, tyrones omnibus ut assuescerent methodis, ut nugae istae semel evanescerent . . . Possunt & Tyrones, si planta in uno alterove systemate non reperiant, mox tertium quartumve evolvere; non enim omnibus Botanicis eadem nota fuere genera."

upon broad evolutive concepts, the presence of connecting links among plants being a gift of Flora to her tired adepts. His mind was early steeped in realities rather than wrapped up in scraps of paper. Had he witnessed the efforts of gentlemen to decide whether an apple is "branch" or "leaf," he would have eaten the apple, I fancy, then asked: "Well, boys, am I digesting a twig or a leaf?"

We have so thoroughly schooled ourselves into believing that Linnaeus is the father of the Dodecandria Trigynia and like amenities that we are seldom aware that he evolved not one, but three systems of classification: (a) the Sexual System, with which his name is unfortunately associated in the mind of most; (b) the Calycinal Method, arranged very much in the manner of the classification of Tournefort; (c) the so-called *Fragmenta Methodi Naturalis*, which are a lasting monument to the Linnean thought.

These three systems are compared and appraised in the pages of the *Classes Plantarum* (1738) as follows:

(a) *Sexual System*. The inadequacy of this system cannot be denied, and is freely acknowledged. It includes as many natural classes and orders as any other system, although exact parallels in this respect may hardly be drawn. Neither this system nor any other may lay claim to being natural.<sup>4</sup>

(b) *Calycinal Method*. The acknowledged purpose of this method is that of giving easy definitions of the calyx [flower] in all its aspects, different arrangements, and characters, this to familiarize beginners in botany with the proper dissection of the floral organs.<sup>5</sup>

(c) *Fragments of the Natural Method*. A truly natural method is the highest goal of systematic botany. Ill-informed botanists believe that such a method has little value, but well-informed ones know that the contrary is true. No one has so far succeeded in designing a true natural method. I [Linnaeus] have labored long trying to work out such a method, and done all I could, without reaching my aim. I will work at this task my whole life, publishing what I shall discover. He to whom it will be granted to perfect a natural method will rank as high as the God Apollo. It is impossible to give a key of the natural method before having placed every plant correctly as to order. It is not enough to define an order using the common characters of its genera, but data must be provided in addition by which one order can be set aside from another. My work is restricted to orders [i.e., families in the modern sense] because once these are correctly placed, the classes [i.e., orders in the modern sense] can be worked out at ease. No a priori rules can be laid down to write a natural method, and no part of the flower and fruit comes first in the sequence of the characters to be used. All that may count

<sup>4</sup> Op. cit. 440. "Classes vel ordines naturales admisit tot, quot ulla methodus alia, numerus tamen genio ubique fruitur suo; obstacula quae methodo contraria erant collegi, candidius imperti; Naturalem methodum nec hanc, nec aliam vocaverim ullam."

<sup>5</sup> Op. cit. 404. "Volui itaque in Tyronum gratiam methodum aliam plane proponere, inque ea Calycis species, differentias, proprietatesque facile omnes primarias describere, uti facilius adsuescerent Calycum dissectionibus Juniores Botanici."

toward such a method is the symmetry of every part, which is often peculiar to each group. Those who endeavor to provide a key to the natural method will be well advised if they pay close attention to the position of the seed in particular. Let everybody correct, extend, and perfect this method who can. Let those leave it alone who cannot. Those who can are the best of botanists.<sup>6</sup>

It is clear from these quotations (many others indeed could be given to the same effect), that Linnaeus had a low opinion both of the calycinal method and of the sexual system; witness the fact that he never used them to instruct the best of his students (see Ventenat, *Tabl. Règ. Vég.* 1: xvii. 1799; Jackson, *op. cit.* 364). His preferences wholly went to the natural method. The high level of systematic thinking which permeates the "*Fragmenta Methodi Naturalis*" in the *Classes Plantarum* (1738) is transparent at a glance through its pages. Order I includes *Arum*, *Dracontium*, *Calla*, *Acorus*, *Saururus*, and *Piper*, possible additions being suggested in certain genera, as yet ill known from the works of Plumier and Rheedee. Order XXVI covers *Theobroma*, *Corchorus*, *Heliocarpus*, *Triumfetta*, *Bixa*, *Clusia*, *Kiggelaria*, *Grewia*, *Tilia*, *Muntingia*, and *Sloanea*, which bears witness to a keen sense of broad affinities. Order XLVII accommodates the Euphorbiaceae with *Euphorbia*, *Dalechampia*, *Clutia*, *Osyris*, *Andrachne*, *Phyllanthus*, *Croton*, *Jatropha*, *Ricinus*, *Acalypha*, *Tragia*, *Mercurialis*, and *Cliffortia*, thus scoring high in a group in which true affinities are not easily detected. Order XX, with *Ficus*, *Dorstenia*, *Parietaria*, *Urtica*, and *Morus*, speaks for itself, considering that a fig and a nettle are not immediately seen to be closely related. Many other Orders can readily be recognized as the fair counterpart of modern families (granted that unwelcome additions are often not lacking) such as Order XXII (Araliaceae and Umbelliferae), Order XXIII (Ranunculaceae), Order XLIV (Rubiaceae). Even where Linnaeus fails, as in Order XIX, containing *Viburnum*, *Tinus*, *Opulus*, *Sambucus*, *Rondeletia*, *Bellonia*, *Cornus*, *Maurocena*, *Cassine*, *Rhus*, *Celastrus*, *Evonymus*, he shows himself a keen student of floral symmetry and structure in the abstract.

<sup>6</sup> *Op. cit.* 484-487, Nos. 1, 4, 7, 8, 9, 11, 12, 13. "Primum & ultimum in parte Systematica Botanices quaesitum est Methodus Naturalis; Hæc adeo a Botanicis minus doctis vili habita; a sapientioribus vero tanti semper aestimata, adhuc licet detecta nondum. . . . Diu & Ego circa methodum naturalem inveniendam laboravi, bene multa quæ adderem obtinui, perficere non potui, continuaturus dum vixero; interim quæ novi proponam: qui paucas, quæ restant, bene absolvitur plantas, omnibus magnus erit Apollo. . . . *Clavis* methodi non dari potest antequam omnes plantæ relatæ sunt ad ordines. . . . Non satis est in definitione ordinis dedisse notas communes, nisi & his intersint, quæ etiam eam ab omnibus aliis distinguant. . . . Classes nullas propono, sed solos ordines, detectis ordinibus, dein in classicis labor facilis erit. . . . Nulla hic valet regula a priori, nec una vel altera pars fructificationis, sed solum simplex symmetria omnium partium, quam notæ sæpe propriæ indicant. . . . Qui Clavem fabricare student, sciant nullam partem universalem magis valere, quam illam a situ, præsertim seminis. . . . Emendent, augeant perficiant hanc methodum qui possunt: desistant qui impares sunt; qui valent, Botanici sunt Eximii."

Enough evidence is at hand to hail Linnaeus as the main founder of the natural method, that is, of true classification. Nor was his thought ill at ease upon the limits between artificial and natural classification, having reached the degree of maturity necessary to draw a sharp line *between description and interpretation*.<sup>7</sup> Linnaeus belongs to us, not to the past. The publication of the *Classes Plantarum* is a landmark of botany, and 1738 a memorable year in our annals.

If Linnaeus so clearly perceived the nature of things past and of things to come, freely admitting that every artificial system was bound to give way as soon as a natural system could be devised (Class. Plant., Praefatio. 1738), why did he not use this system in his works?

The mind of certain men is so ultimately gifted and so all-pervading that these men are inclined to see any important issue *sub specie aeternitatis*, as it were, making light of the present in anticipation of the future. Linnaeus had probed the difficulties inherent in a natural method, and come to the ultimate conclusion that such a method could not be brought into flower until the tides of time should return over and over again to the same shores. How correct he was we know, who still feel that a natural system is not wholly within our grasp. Other men, not less gifted and perhaps not less profound, cater to the present, feeling that every day is sufficient unto itself, and that to the individual *mors est ultima linea rerum*. To decide between these two philosophies, and to judge of the ultimate greatness of all these men is not easy, although many, among them myself, are ready to hail active imperfections in preference to ever deferred perfection. All we may say is that, broadly speaking, Linnaeus could probably not put up with active imperfection, being great enough, however, to school others in its use and limitations.

As a teacher, Linnaeus, moreover, must have felt, like another competent teacher, Amos Eaton, that the Sexual System had temporary value *as an artificial key*. Quoth Eaton (Man. Bot. North Am. ed. 6. 1: 13. 1833): "The object of the Artificial system is merely to furnish a method for ascertaining the name of a plant. The object of the Natural system is to bring together into small groups, plants which resemble each other in their botanical affinities, sensible qualities and medicinal properties. The Artificial sys-

<sup>7</sup> Little less mature, if indeed at all, was the Linnean thought of 1737 on the limits between description and pure nomenclature. In his condemnation of redundant descriptive polynomials (Crit. Bot. 152. 1737; Phil. Bot. 204. 1751) Linnaeus laid down principles which, somewhat more stringently applied, had as their result the adoption of binomial nomenclature in 1753. The advantage of adopting binomials or short polynomials had not gone undetected, witness the catalogue of the Botanical Garden of Bologna, Italy (*Hortus Studiosorum Bononiae Consitus*), prepared and published by an obscure professor of botany, Ambrosino, in 1657. Linnaeus is the genius, however, to whom it was given to think himself out on principles before advancing concrete solutions. This lucidity of thought is the secret of his hold upon generations of naturalists.



tem has been very aptly compared to the dictionary, and the Natural, to the grammar of a language." To this Eaton added (op. cit. 1: viii. 1833): "The Natural Method should engage the attention of the student, after he has become acquainted with about 400 species of plants, by the aid of the Artificial Method."<sup>8</sup> Eaton's opinions closely agree with those of Jaume-St. Hilaire (Pl. France 1: xxiii-xxvii. 1805), written a full quarter of a century before. That Linnaeus meant the Sexual System as an artificial key can readily be seen. In the *Classes Plantarum* (1738) *Ficus* is properly entered in Order XX of the "Fragmenta Methodi Naturalis" (op. cit. 494), together with *Dorstenia*, *Parietaria*, *Urtica* and *Morus*, as we have seen. In the *Systema Sexuale* exhibited in the same work (op. cit. 483) *Ficus* is set out precisely where a beginner, not a botanist, would look for it, in the *Cryptogamia*, alone under *Plantae*. In the *Methodus Sexualis* (1737), appended to the *Genera Plantarum*, the same genus is freely shifted among different Classes and/or Orders if its sexual characters warrant it. Accordingly, *Rhamnus*, which in the *Classes Plantarum* (1738), is firmly kept under Pentandria Monogynia, is tossed about in the *Methodus Sexualis* (1737), as Pentandria Monogynia (its main position) Pentandria Trigynia, Dioecia Tetrandria, and Polygamia Dioecia. Since examples of this nature could be multiplied, nothing should be easier than to prove that Linnaeus was "inconsistent" in his handling of the Sexual System, and could hardly draw the line between a toadstool and a fig. Such a "proof," however, would merely show that its author knows nothing, convincing as the "proof" might be in point of fact.

Against Linnaeus and all his predecessors Adanson had a thesis to establish. The thesis was that all artificial methods were worthless, and that only the natural method could be used. Like Robert Brown, Adanson had travelled in the tropics, and there realized that the classifications of Tournefort,

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<sup>8</sup> Eaton happens to be the author of a Natural Method of his own. Incensed by De Candolle's and Lindley's treatment of Jussieu as an "ordinary fellow laborer" (op. cit. 1: iv), and believing that the aim of these systematists was "the total annihilation of the system of Jussieu" (op. cit. 2: 3), Eaton reinstated the old Jussieuan names. He still called them orders, but used them sometimes as we do families. The outcome of Eaton's concern with justice and priority is baffling, to say the least. He divided, for instance, the "ORDER L. *Rhododendra*. LI. *Ericae*" into three groups of undefined rank, Ericaceae, Vaccineae, and Pyrolaceae, subdividing the former into Ericaceae verae and Rhodoraceae. The Order Berberides (op. cit. 2: 104) he subdivided into Berberideae and Hamamelideae, the Order Magnoliae (l.c.) into Magnoliaceae and Wintereae. His treatment of the magnoliaceous group is factually the same as that of De Candolle (in DC. Prodr. 1: 77-79. 1824), who published the Magnoliaceae as a family (*Ordo* of De Candolle) with two tribes, Illicieae and Magnolieae. Contrariwise, the Berberides, as understood by Eaton, are meant as an order in the modern manner, that is, as a group of presumably allied families. Eaton proved unable to extricate priority from systematic concepts, but his concern with the units above the family, and his insistence upon older names, are not lacking in a constructive side. Bartling had at long last carefully described these units only three years before (1830), and Lindley was still to write about them three years later (1836). Eaton's Method seems to have been overlooked by nearly all indexers.

Linnaeus, and others were hopeless in the face of new aspects of nature. From his travels, and by lifelong study, he had reached the conclusion that plant distribution spoke a definite language to the systematist, and that the very concepts of the units used in classification should be redefined. This, and much else which space forbids me to mention, Adanson plainly states in his monumental preface to *Les Familles des Plantes* (1: clvi, clxvii, *et passim*. 1763), a work of lasting erudition, if not of dispassionate judgment. Unlike Linnaeus, Adanson had the soul of a philosopher inclined to take immediate action. As a clever polemist, but not as an unbiased critic, he dismissed everything which Linnaeus had done as too artificial or inconsequent (op. cit. 1: xlii, xliii, xlv, xlvii), lumping together beyond the claims of justice as of one cloth the sexual system, the calycinal method, and the fragments of the natural method. That Adanson, enriched by his experiences as an explorer and as a thinker, had to broadcast his message in the face of sloth or actual opposition may induce us to forgive the poisonous sting of some of his comments, his boast that only three of his sixty-eight families, *Vaccinia*, *Cisti* and *Ara* (op. cit. 1: excix) were not satisfactory, his lavish incorporation of doubtful or ill-known genera, and his flagrant breaches of good taste in priority.

Strange to say, the thought of Adanson had much in common with that of Linnaeus. Both these masters worshipped the natural method, and each gave us the outline of one. Both felt the need of artificial systems, or keys, of which Linnaeus gave us two, and Adanson sixty-five (op. cit. 1: cccxi-cccxi). Both were hampered by lack of material and lack of knowledge. Coldly appraised by a systematist, the "familles" which so much pleased Adanson are readily seen not to be much better than the "fragmenta" which Adanson despised; witness, for instance, the content of the Tithymali of Adanson (op. cit. 2: 354-358), and that of the Order XLVII of the *Classes Plantarum* of Linnaeus, later to become with some unwelcome additions the Tricoccae of the *Philosophia Botanica* (32. 1751).<sup>9</sup> Considering the level at-

<sup>9</sup> The name Tricoccae (or Tricocca), together with several others which appear in the Linnæan "Fragmenta Methodi Naturalis," is taken from Van Royen's *Florae Leydensis Prodrromus* (1740), with or without very slight changes in the endings. A glance at the twenty Classes of Van Royen will readily convince a critical reader that Linnaeus owes little to him beyond occasional nomenclature. Van Royen had an understanding of natural classification, which the preface in his work reveals, but, very much like Ray, fell into error, carefully pointed out by Linnaeus, to attempt to define the Class (modern order) before the Order (modern family). The result is that the Aggregatae of Van Royen include under two subdivisions, Monopetalae and Pentapetalae, such genera as *Protea*, *Conocarpus*, *Cephalanthus*, *Morinda*, *Dipsacus*, *Scabiosa*, *Knautia*, *Dorstenia*, *Globularia*, *Lagoecia*, *Jasione*, *Brunia* and *Statice*. The Incompletae of Van Royen are a fantastic mixture of *Salicornia*, *Empetrum*, *Dodonaea*, *Hippophae*, *Celtis*, *Potamogeton*, *Chara*, *Thesium*, *Hedera*, *Buscus*, *Alchemilla*, *Hura*, and the like. Certain of the Classes of Van Royen are much better than others, some, like the Tricoccae, almost natural. However, it is not so much the casual right or wrong guessing that stamps the true systematist, as the quality of his thought as a whole. As a thinker, Van Royen does not begin to compare with Linnaeus, and is below Adanson, Lamarck, and A. L. de Jussieu.

tained by botany in 1738 and 1763, it is not surprising that Linnaeus and Adanson should break about even in systematic performance. To Adanson credit must be due, however, in several respects: (1) By his uncompromising rejection of the very principles of artificial classification, Adanson focussed the attention of the botanical world upon the need of proceeding with natural classification in a positive rather than in an abstract manner. To this extent, Adanson had most likely a powerful influence upon Bernard and Antoine Laurent de Jussieu, the Apollo of the natural method.<sup>10</sup> (2) Adanson provided description of groups more or less akin to modern families or orders, and of their major subdivisions, whereas Linnaeus had written only series of generic names under undescribed orders. (3) Lastly, Adanson soared to a perception of the vastness and complexity of the kingdom of plants, from this deriving conclusions of value to the botanist in various fields. Perhaps too little credit has been given him in this respect. Hasty perusers of the *Familles des Plantes*, repelled by a unique spelling of Adansonian concoction and untold barbarous generic names, all too readily conclude that Adanson is a crackpot. Such a conclusion is absolutely erroneous, for Adanson soars high among the masters of botany. So much could easily be proved, if space did not forbid my delving further into Adansonian thought here.

The ground had been thoroughly laid by Linnaeus and Adanson to use natural classification in 1763, but the joint significance of the work of the two masters seems to have been lost on their immediate contemporaries. Bernard de Jussieu, their most receptive listener, published nothing of botanical significance, leaving it to his nephew Antoine Laurent to pick up the good trail about a quarter of a century later. Five years after the publication of Adanson's *Familles*, and Linnaeus's second edition of the *Philosophia Botanica*, Haller released his *Historia Stirpium Indigenarum Helvetiae* (1768), a work which contains (1: xxv-lviii) a laborious superb bibliography. Haller comments (op. cit. xxii) that he could have saved himself a great deal of labor had he chosen to follow the Linnean classification, meaning by this the sexual system. However, Haller confides, this was too much for him to do, considering that Linnaeus had torn to shreds even the most natural groups, as the *Gramineae*. So as not to follow Linnaeus, Haller drew

<sup>10</sup> Strong evidence is at hand that Adanson might have had more than influence upon Bernard and Antoine Laurent de Jussieu. The seldom read second edition of the *Familles des Plantes*, edited by Alexander Adanson & Payer, contains a parenthetical statement (1: 134. 1847), evidently culled from Adanson's original manuscript, in which the latter affirms that the outline of the *Familles*, sent with full details to Bernard de Jussieu in 1750 from West Africa, had never been returned, either by Bernard or by Antoine Laurent. This statement does not appear in the original edition (op. cit. 1: cc), which is good evidence of Adanson's love of truth rather than quarrels. On points involving fact, and even more tendencies, Adanson was outspoken, occasionally rash. On matters of precedence and personal satisfaction he could hold his peace.

up his own "Systema," hoping thereby to keep intact as many natural groups as possible. Since this "Systema" is artificial, Haller was fated to fail in his attempt at building natural groups. His key (Tabula Classium et Generum) is by no means easy to handle; one of the groups under Classis I, which includes the Compositae, is made of the genera *Senecio*, *Solidago*, *Aster*, *Erigeron*, *Doronicum*, and *Arnica*. Had Haller turned to Adanson's *Familles* he would have found therein "Famille XVI. Les Composées. *Compositae*," a close match of Linnaeus' "Compositi" (Phil. Bot. ed. 2. 33. 1763). His group Haller would have found, moreover, fairly well represented by Adanson's "VIII. Section. Les Jacobées. *Jacobeae*" (op. cit. 2: 123), and included under Linnaeus' "*Compositi Corymbiferi*" (loc. cit.). Using any of these names with some emendation, Haller could have saved himself the trouble of erecting a new "Systema," and given partial keys to his satisfaction. In fairness to Haller, it must be said that the botanists of the day could not think this simple way, and that the efforts of Linnaeus and Adanson were still gems in the rough. So much, however, does not detract from the fact that natural classification was already alive in 1763, and that a creative mind could with little effort free himself by then of the stifling belief that describing rather than understanding is the soul of science.

Gleditsch's *Systema Plantarum a Staminum Situ* (1764), is characteristic of a form of thought for which the Linnean *Fragmenta Methodi Naturalis* of 1738 did not exist. New terms are used in this "Systema," the *Phaenostemonis* replacing the *Phanerogamia*, and the *Cryptostemonis* the *Cryptogamia*, but, as one would expect, the old wine still fills the old skins. *Cactus*, as manipulated by Gleditsch (op. cit. 274), aligns itself with *Mesembryanthemum*, *Eugenia*, *Philadelphus*, *Psidium*, *Myrtus*, *Punica*, *Crataegus*, *Sorbus*, *Mespilus*, and *Pyrus*; and *Euphorbia*, enthroned in the *Thalamostemones Dodecantherae*, is satisfied to rest (op. cit. 105-107) with *Rhizophora*, *Garcinia*, *Crataeva*, *Triumfetta*, *Peganum*, *Nitraria*, *Portulaca*, *Heliocarpus*, *Reseda*, *Menispermum*, *Illicium*, and *Sempervivum*. With this, everything is back at least to the early days of Tournefort.

LAMARCK, A. L. DE JUSSIEU, VENTENAT and NECKER

The *Flore Française* published by Lamarck in 1778 is striking in being written throughout as an artificial key. The preface of this work is remarkable. In it, an artificial key is represented as something wholly unlike true classification. The thought is not new, as we know, following as it does Linnean lines of 1738. However, unlike Linnaeus, Lamarck draws rigorous, practical conclusions. He points out (op. cit. 1: lix) that an artificial method, or key, can have no other purpose than yielding the name of a plant already described. The basic principles for the making of a good key, Lamarck states, are two: (a) every character must be made use of, so far as possible, with the

exception of those which are not readily apparent; (b) the descriptions in the key must be clean-cut, and the key-groups sharply defined. Lamarck comments upon the second principle (op. cit. 1: lx-lxi) characteristically as follows: Since it is patent that the key-groups are bound to violate somewhere even the sharpest natural affinities, we must set our minds at rest, accepting the fact that these affinities will be disregarded as a matter of course. Nothing else counts for so much as a method of keying which establishes hard and fast groups, and leads to describing them in an unequivocal manner. It is immaterial that these groups cut through natural affinities.<sup>11</sup> Fully as lucid are the principles which Lamarck lays down to write botany along natural lines. These principles (op. cit. 1: xcii) are (a) to determine which plant is to come first, as initial in a natural series; (b) to provide rules whereby the species can best be brought together; (c) to lay down a consistent line of treatment for orders and families which cannot be broken into lesser units. Lamarck concludes in what is to us a strange vein (op. cit. 1: cxviii), saying that so poor is the flora of France that it can best be treated only under the artificial method, that is, by a key. Naturally treated, Lamarck argues, the flora of France would be riddled with gaps.

To us, who are thoroughly aware of the essential difference between a key and classification, Lamarck's comments sound anything but revolutionary. To Haller, to Gleditsch, and to the multitude who still strove to mix description and interpretation, concocting artificial keys that should be factual classification, Lamarck's warnings were thunderbolts. That which Ray had felt Linnaeus passionately preached in low tones, Adanson stated in a rasping voice, and Haller and Gleditsch never understood, Lamarck laid down in a masterly hand as common sense, which of all human weapons is the most powerful in the long run. Wholly to the point, if beyond the truth of history, A. P. De Candolle hailed the *Flore Française* (Fl. Franç. ed. 3 1: vii. 1805) as the first work in which the soul of the natural and artificial method had been laid bare. Linnaeus in his *Classes Plantarum* had indeed been first to see clearly the light, but Lamarck had been second to none in carrying this light to its ultimate limits. Lamarck thoroughly uproots the hoary confusion between description and interpretation, between mere key making and genuine systematic thinking. Unknown to most, the year 1778 looms large in the annals of botanical thought.

In the *Genera Plantarum* (1789) of Antoine Laurent de Jussieu description and interpretation are kept apart in the best Lamarekian style. Jussieu recognizes a hundred "Ordines Naturales," more or less agreeing with

<sup>11</sup> "Ayant reconnu qu'on ne peut faire une seule division qui ne rompe quelque part des rapports très-marqués, on doit se mettre parfaitement à son aise sur cet objet, s'occuper uniquement de la sûreté de la méthode, former des divisions tranchantes & circonscrites par des définitions à l'abri de toute équivoque, sans avoir égard aux séparations frappantes que ces divisions peuvent occasioner."

families in the modern sense, and fifteen "Classes." The classes are keyed out in one page (op. cit. lxxi), the key resting upon a division of plants into Acotyledones, Monocotyledones, and Dicotyledones, and lesser groups based upon peculiarities of the corolla and the stamens. The orders are dealt with at length, but not keyed. The sharp eye of Antoine Laurent realized, no doubt, that some classes were natural, like No. XII, including Araliaceae and Umbelliferae, while others were not, like No. XV, associating the Euphorbiaceae with the Cucurbitaceae, Urticaceae, Amentaceae, and Coniferae. However, the classes bore no name, and were non-committal, as we now say, hardly better than artificial or occasionally natural key-groups. Altogether different was the case with the Orders, which Jussieu strove to maintain natural throughout. In the *Flore Française* Lamarck had chosen to abide by a key, without using natural classification; in the *Genera Plantarum*, Jussieu used both a key and natural classification. In this Jussieu consciously set a precedent, a far-reaching one, considering the fundamental nature of the *Genera*, and its immediate acceptance by the best botanical minds of the time.

Behind Lamarck and Antoine Laurent de Jussieu, looms large the silent figure of Bernard de Jussieu. While Adanson was busily writing, and Linnaeus in part theorizing, Bernard acted in the most direct and unpretentious manner. As Antoine Laurent tells us (op. cit. xxxvi, xlix, lxiii-lxx), Bernard in 1759 laid out the plants of the royal garden at the Trianon according to the natural system. Later on, in 1774, the same plan was introduced in the botanical garden of Paris, and on this the *Genera* was patterned. The natural system of Bernard de Jussieu closely followed the lines of Linnaeus's *Fragmenta Methodi Naturalis*, and Adanson's *Familles des Plantes*, which can readily be seen by comparing, for instance, the *Sempervivae* of Bernard (op. cit. lxix) with the *Succulentae* of Linnaeus (*Phil. Bot.* ed. 2. 36. 1763) and the *Portulacae* of Adanson (*Fam. Pl.* 2: 235. 1763).

Bernard's quiet deed powerfully influenced botanical thought. Linnaeus's bold stroke had popularized the study of botany in 1735 by introducing the sexual system, and Bernard's arrangement in 1759 made it possible for every thinking botanist to see the natural method of classification at work. Such a person could leisurely walk through the alleys of the Trianon, and of the botanical garden of Paris, think his own thoughts, leave, and return. Since thought feeds on observation, and ideas come at leisure, mostly to those who choose to live with plants rather than to finger them only in an herbarium, Bernard's exhibits gave to everybody who cared to listen a lecture of the most objective and cogent sort. As new plants came in, from distant or from near lands, it was natural that they should be fitted into the frames of the natural system, for this system every French botanist had in mind. As the pieces of a puzzle are sorted and shifted, so were new plants set under this or that order and group, each increase in knowledge making it

easier to deepen and to elaborate the system. It was known within thirty years that the Succulentae of Bernard actually fell into six natural groups, which Antoine Laurent published as the Succulentae, *sensu stricto*, the Saxifrageae, the Cacti, the Portulacae, and the Ficoideae. Others could theorize about these groups in Germany, Italy, or England; in France *they had seen them*. The objective method of dealing with vegetables inaugurated in Paris insured the preeminence of French systematic thought at a critical moment in the history of botany. Could we follow a like method, creating a center of botanical endeavor where plants can easily be grown, and be thought upon as they grow, we would insure, no doubt, felicitous results, for neither nature nor man does change.

Adanson had the manuscript of the *Familles des Plantes* available in 1759, and the fact that Bernard de Jussieu laid out the plants of the Trianon in a natural manner the very same year may not be a coincidence, as we have seen. Through the *Classes Plantarum* (1738) the *Familles des Plantes* (1763) and the *Genera Plantarum* (1789) runs the same thread. Bernard de Jussieu published nothing which a botanist is supposed to know about, but without him Antoine Laurent could hardly have written the epochal *Genera Plantarum*.

The thought of Necker has weighed heavily upon many consciences, my own not excluded (Croizat & Hara in Jour. Jap. Bot. **16**: 384. 1940). Yet, when it is seen as part of a larger whole, this thought yields up most of its mysteries. Here was a man of prodigious industry but confused thinking, for whom neither Linnaeus nor Adanson had ever written a creative word. His *Elementa Botanica* (1790) is unadulterated artificial classification to be used as a key (op. cit. **1**: xvi–xvii *et passim*). Like every uncreative mind, Necker felt the greatest need for new words, to take the place of new thoughts. Accordingly, Linnaeus' Compositi and Adanson's Compositae would not do, but the "Genus" Actinophytum had to be coined instead. Aware of the artificiality of the Linnean Sexual System, but conscious, as it seems, that the Linnean genus was a tolerably natural group, he decided to call "genera" units above the commonly accepted genera, which units he thought, mayhap, to be natural.<sup>12</sup> Under these he set out the "Species

<sup>12</sup> This notion may not even be original with Necker. Ray had spoken (Meth. Pl. Emen. Praecognoscentia. 1703) of "Genera summa . . . subalterna & infima," and designated his main units as "Genera." In 1737 Linnaeus had admitted (Crit. Bot. 138. 1737) that the class (modern order) could be understood as "Genus summum," and the order (modern family) as "Genus intermedium." As if sensing the danger that this admission could be misunderstood and abused, Linnaeus carefully reworded it in the *Philosophia Botanica* (136. 1751), as follows: "Quod valet de caractere generico, valet etiam de classico, licet in hoc latius sumantur omnia. Generum genus est Ordo, ordinum autem genus Classis est." This revision might have come too late; it is likely that Necker decided that the "Genus intermedium" could be deprived of its qualifying adjective, and left as Genus, a tail in the shape of the adjective Naturalis or Immortalis being affixed meanwhile to the Species. Some souls cannot withstand temptations of this sort.

Naturalis" or "Species Immortalis," which by being a group of related species could be little else but a genus in the Linnean sense. The "Prolis" was the individual plant. The results of these manipulations are dismaying, and it seem altogether likely that Necker himself, having been formed as a botanist in the Linnean school, could never fully eject from his subconscious the Linnean units, while mixing them up with his novelties. One who does not well know what he wishes to say may always be quoted in any way a commentator likes, and Necker may be presented, perhaps, both as a genius and as a crackpot by parties willing to make convenient abstracts from his lucubrations. The fact that he can be made to play both roles, while certainly yielding nothing creative, shows Necker to belong with the crackpots rather than with the geniuses. If we turn to his *Elementa*, (3: 102-122. 1790) we find, for instance, the "genus" Daphnophytum which includes *Ceratocarpus*, *Cynomorium*, *Gunnera*, *Antidesma* (*Stilago*), *Hura*, *Salacia*, *Nepenthes*, *Aristolochia*, *Osyris*, *Elcagnus*, *Gouania*, *Bucida*, *Waldschmidtia*, *Conocarpus*, *Saraca*, *Pistia*, *Cytinus*, *Asarum*, *Tamus*, *Rajania*, *Hippophae*, *Theligonum*, *Viscum*, *Datisca*, *Terminalia*, *Nyssa*, *Stratiotes*, *Montinia*, *Casuarina*, and *Aegopricon*. This list speaks for itself, and if Necker happens to concoct a "genus" which is natural it is certainly Nature's fault. Since Necker was fond of small units, in the "Species Naturales" he set out, no doubt, "species" of the kind which contain the ghost of a good genus. His *Aroton* may well be *Caperonia*, his *Cratochwilia* is perhaps *Bridelia*, his *Arachne* is *Sauropus*, his *Athymalus* is the segregate of *Euphorbia* which Haworth later called *Dactylanthus*. All these "species" have priority in the Euphorbiaceae, but, to forget the safety valve offered an harassed taxonomist by the *nomina generica conservanda*, the plain truth is that these names are illegitimate, because they subvert the prescribed sequence of the units of classification. If we honor these "species," we might as well honor "genus" Daphnophytum, typifying it through allegories and fictions. A simpler solution is that those who formally leave the botanical fold be kept out of it, if this happens to be legal. The matter is not offered here for immediate discussion, because only the value of Necker's systematic thought is in question. On the score of this value few indeed will be found to disagree.

#### TRIMMING AND POLISHING

With the publication of de Jussieu's *Genera* in 1789 the period lasting from 1738 to 1790 comes to an end, in which true classification extricates itself from the thralldom of key-making, and interpretive systematic botany triumphs, in principle, over descriptive taxonomy. The period that opens in 1790 is essentially concerned with three phases of endeavor: (a) defining the units above the family; (b) defining the units between the family and the genus; (c) providing a suitable nomenclature for these units.



Of these three undertakings the first was fated to come to the fore later than the two others. So long as the affinities between families were poorly understood, few indeed would worry about the concepts and the names which might apply to the order and to the class. To determine the fate of the units between the family and the genus was more urgent, and it was not less urgent to name properly the families and their subordinate units.

Linnaeus had adopted special names for his "Fragmenta" in the first edition of the *Philosophia Botanica* (1751) such as Vepreculae, Scabridae, Cucurbitaceae, Tricoccae, also retaining traditional designations like Palmae, Coniferae, Compositi, and the like. Adanson preferred to use almost exclusively the plural of some characteristic generic name, turning the French vernacular designations "les cistes," "les airèles," "les pourpiers," for instance, into their pure Latin equivalents, *Cisti*, *Vaccinia*, and *Portulacae*. Unlike Linnaeus', Adanson's nomenclature was marred by ambiguity, for "les cistes," *Cisti*, could be understood to mean certain species of *Cistus*, or the group, or family, which Adanson had erected around *Cistus*.

Between 1763 and 1825, the French had a factual monopoly of natural classification, and certain aspects of the nomenclature of the family cannot be understood unless account is taken of French linguistic peculiarities and uses. To us, terms like the Cactaceae, the Euphorbiaceae, the Taxaceae are part and parcel of the *English* botanical tongue, for we have no vernacular equivalent with which to replace them. Not so with the French, who would refer to the "Cactées," "Euphorbiacées," and "Taxacées" as a matter of course, and use the Latin forms of these names only in strictly formal work. In creating names for families and like units, the French coined as a rule the French term first, later translating it into Latin. The result of this linguistic quirk was that, in all too many cases, French euphony prevailed in the matter of name-giving. It is not clear to us, for instance, why Jaume-St. Hilaire should have rejected the name Onagrae of Adanson and Jussieu (*Expos. Fam. Nat.* 2: 148. 1805) in favor of a new Onagrariae. The only possible explanation for this departure from accepted endings is that "Onagraires" is more agreeable to a French ear than "Onagrées" or "Onagracées." Even an ill-sounding name is acceptable when it has been in constant use, but French authors between 1789 and 1825 were coining *new* names, and with them euphony, even as individually understood, rated as no paltry consideration. Rules of nomenclature with binding power they had none. The elder De Candolle, for instance, gave a false reference to the "Magnoliacées Juss. gen., 280" and the "Annonacées Juss. 283" (*Théor. Elém. Bot.* ed. 1, 213. 1813) for the same reasons; Jussieu had published, in truth, the Magnoliae and the Anonae. The Code of Paris, of 1867, maintained the Ordo and the French term Famille as synonymous partly on these same grounds (*Lois Nom. Bot.* 1867: 15; Comm. 34. 1867), which proved unfortunate.

The proper nomenclature of the family was dealt with by the elder De Candolle in his *Théorie Élémentaire de la Botanique* (247, 1813; ed. 2, 276-278, 1819). He accepted the ending *-aceae*, praised as good forms Liliaceae, Rosaceae, Anthirrineae, Ericineae, and Laurinae, disapproved of the endings in *-oideae*, and suggested that such names as Salicariae, Thymeleae, and Frangulaceae should be used in certain cases. In 1819 (op. cit. 278) he advanced a nomenclatural innovation to forestall ambiguity between the name of a family and that of a tribe. The name of a family should be derived from the name of an important genus under it made longer by one syllable, witness Ranunculaceae, Myrtineae, Flacourtianae; that of a tribe merely by making an adjective as Ranunculeae, Myrteae, and Flacourtiae. It will readily be seen that these rules left euphony free play, although they tended to set up a factual standard for the publication of tribal names ending in *-eae*. Plural generic names could be tolerated only if they cause no ambiguity.

Antoine Laurent de Jussieu had given little thought to nomenclatural amenities. He had retained traditional names (Palmae, Coniferae, Cruciferae, etc.) together with plural generic designations in the Adansonian tradition (Asparagi, Asphodeli, Narcissi, etc.), names ending in *-aceae* (Campanulaceae, Rubiaceae, Papaveraceae, etc.), in *-eae* (Borragineae, Polygoneae, Jasmineae, etc.), in *-oideae* (Aroideae, Cyperoideae, etc.). Ventenat rejected much of this loose nomenclature (Tabl. Règn. Vég. 1799), intending to do away with generic plural names of Adansonian flavor, and to standardize the endings somewhat. Accordingly, he replaced the Pediculars of Jussieu with his own Orobanchoidae and Rhinanthoidae, the Euphorbiae with the Tithymaloideae, the Guaiacanae with the Ebenaceae, the Rhododendra with the Rhodoraceae, the Plantagines with the Plantagineae. Ventenat reinstated in addition certain ancient Linnean names, such as the Bicornes for Jussieu's Ericae, and himself introduced like names; witness the Hilospermae to replace Jussieu's Sapotae, the Glyptospermae instead of the Anonae.

Since neither A. P. De Candolle (Fl. Franç. ed. 3, 1805) nor Jaume-St. Hilaire (Exp. Fam. Nat. Pl. 1805<sup>13</sup>) liked endings in *-oideae*, they ruled out Ventenat's Tithymaloideae, replacing it with the Euphorbiaceae, and so on.

<sup>13</sup> These two important works were both published in 1805, "An XIII." Their priority is to be settled as follows: (1) *Jaume-St. Hilaire*. Actually published in *March, 1805* (See Intelligenzbl. Allg. Lit.-Zeitung 1805: 427. 1805, offering the work for sale before April 3rd; Jour. Gén. Litt. France 1805: 36. 1805). (2) *Lamarck & Decandolle*. Actually published in *September, 1805* (See Jour. Gén. Litt. France 1805: 260. 1805). The publication was intended for the beginning of the year, but delayed by corrections (op. cit. 261). This may account for Labillardière's statement, dated July 8th, 1805 (in Ann. Mus. Hist. Nat. 6: 451. 1805, XIII), carrying an implication that the work in question was by then already out of press. It may be added that the references here cited are a ready source of valuable data for the actual dates of publication of most works credited to this period.

We must come to the first volume of De Candolle's *Prodromus* (1824) to find a beginning of true standardization, with family names ending in *-aceae* (Ranunculaceae, Dilleniaceae, Magnoliaceae, Anonaceae, Podophyllaceae, etc.), in *-eae* (Berberideae, Capparideae, Flacourtiaceae, Bixineae, etc.) together with some ancient designations like Cruciferae. The subdivisions of the family are tribes standardized mostly to end in *-eae* (Illicieae, Magnolieae, Lardizabaleae, Menispermaceae, etc.). This is the nomenclature still followed, in the main, in Bentham & Hooker's *Genera Plantarum* half a century later.

The family, as we understand it, was mostly designated as Ordo, which was the old Linnean designation of the "Fragmenta." The unit below the Ordo was the Sectio, named or unnamed, in the works of Adanson, Ventenat, Jaume-St. Hilaire. However, De Candolle designated as Ordo as late as 1805 (Fl. Franç., ed. 3. 3: 318, 321) the Sectio of other authors, publishing for instance the "famille" Urticeae with two "Ordines," Artocarpeae and Urticeae. In 1819, De Candolle had changed his mind, and used the rank Tribus for the same category.

In conclusion, when systematic botany began to leave France, the following had been achieved: (a) the "Subclassis" (equivalent to the current Suborder) had gained nomenclatural recognition with the Thalamiflorae, Calyciflorae, etc., of De Candolle; (b) the "Ordo," no longer a Tribe, but matching the current Family, had been standardized around endings in *-aceae* and *-eae*, some traditional names being retained throughout as the Cruciferae; (c) the "Tribus," embracing our own Subfamily and Tribe was firmly rooted in endings in *-eae*. We must come to Lindley, in the classic *Natural System of Botany* (1836<sup>14</sup>) to find a full standardization, the "Alliances" (modern Orders) ending in *-ales*, and the families in *-aceae*. This standardization, of course, was no more accepted by all than had been the nomenclature of De Candolle. The Code of Paris of 1867 left the field practically wide open. It stated that the families should end in *-aceae* (Art. 21), but authorized numerous exceptions on the ground of usage, legitimizing for instance (Art. 22) the Salicineae, the Berberideae, the Tamaricineae, the Dipterocarpeae, the Lentibularieae, in addition to the Compositae, the Labiatae and the like. The subfamilies ("subordinates, subfamiliae") should end in *-eae* (Art. 23), the tribes and subtribes (Art. 24) in *-eae* or *-ineae*. The section dealing with the names above the genus is possibly the worst in the Code of Paris, attempting as it does to indorse almost every use and abuse under cover of long previous custom.

The omission from these pages of any reference to botanical thought in the United States is not accidental. As a matter of fact, the history of this

<sup>14</sup> This is the second edition. I have not been able to consult the first, which appears mostly to follow the Candolleian classification.

thought is so interesting that justice may be done it only in the course of an extensive review. If Nuttall rates as an American, this country can readily be shown to have been not inferior to England in constructive systematic thinking between 1800 and 1830. Under the thin veneer of the Linnean Sexual System, which he fully rejected as early as 1825 (*Jour. Acad. Nat. Sci.* 5: 132), Nuttall contributed in 1817 (*op. cit.* 1: 111) searching discussions of natural affinities. In a work with the outward appearances of artificial classification, but as thoroughly imbued with Jussieuan spirit as Jussieu's own writings, Nuttall was the author of such groups as the *Monotropeae* (*Gen.* 1: 272. 1818) and the *Empetreae* (*Gen.* 2: 233), which were readily received by the progressive botanists of Europe. Nuttall's pedagogic work (*Intr. Syst. Physiol. Bot.* 1827) has a sweep and vigor of treatment which is not apparent in many of the writings of his contemporaries, and reveals him as a master of limpid thought and conscious purpose.

#### NOMENCLATURAL CONSIDERATIONS

The Rules of Vienna (1905), still in vigor in this respect, prescribe (*Art.* 23, *Amsterdam Rules*, 1935) that the name of a family must be derived from that of a present or former genus and must end in *-aceae*, allowing exceptions in favor of the traditional designations *Palmae*, *Cruciferae*, *Compositae*, and the like. Subfamilies (*Art.* 24) are to end in *-oideae*, tribes in *-eae*, and subtribes in *-inae*, all names to be derived from those of genera. The names above the family are left to a Recommendation (*Rec.* ix), advising that the Orders end in *-ales*, the Suborders being variously named, *Tricocceae*, for instance, but preferably ending in *-incae*.

To analyze these Rules in detail is not the purpose of this study. I will point out here merely two cases which deserve immediate attention, and voice my opinion on their possible solution:

(a) A very great number of names with the above endings have been published by authors under ranks which make the endings untenable under the current Rules; witness Ventenat's *Tithymaloideae* announced as an order, but acceptable only as a subfamily; De Candolle's *Artocarpeae* published as an "Ordo" under a family, but with an ending legitimate for a tribe.

(b) Many names published by French authors in the French language have been latinized by later writers, witness the "*Perideae*" credited to Baillon by Pax & Hoffmann (*in Engl. & Prantl, Nat. Pflanzenf. ed.* 2, 19(c): 153. 1931), whereas Baillon spoke of the "*Péridées*" (*Ét. Gén. Euphorb.* 433. 1858).

If we turn to authoritative literature for guidance, we find therein the most appalling confusion. German work, which is still our readiest source of reference for the nomenclature of units above the genus, can hardly be trusted. Engler & Krause (*in Engl. & Prantl, Nat. Pflanzenf. ed.* 2, 19(c):

1. footn. 1931) comment on the Chailletaceae and the Dichapetalaceae in a manner which reveals total unfamiliarity with the rudiments of correct nomenclature, and shows that they are not aware that a family name may be conserved. Pax & Hoffmann (op. cit. 44) treat the Phyllanthaceae, a tribe of Bentham & Hooker, as an exact synonym of their own subfamily Phyllanthoideae, and maintain their own, and later, tribe Phyllanthaceae as legitimate. They, likewise, (op. cit. 89, 96) erect two subtribes, Regulares and Irregulares, under tribe Crozophoreae, in violation of the Rules concerning the proper ending for this category. Engler's Syllabus, ed. 8, 1919, accepts two subfamilies of Schumann, the Pereskioideae and the Cereoideae under the Cactaceae, which is as it should be. However, in the 9th/10th edition of the same work (1924) these two subfamilies are replaced by two new subfamilies of Vaupel, the Malacospermae and the Sclerospermae, formally incorrect in endings, worthless from the systematic point of view, and untenable as to priority. Vaupel's clean-cut affirmation that priority has no place in the classification of the Cactaceae (in Engl. & Prantl, Nat. Pflanzenf., ed. 2, 21: 613. 1925) must be seen to be believed in. In these, and countless other abuses of every nomenclatural principle, is clearly read the notion, known only to some outside of Germany, but there to all appearances widely current, that the names above the genus do not apply to anything in particular, and may be handled at will.<sup>15</sup> It is not surprising that most modern authors upon dealing with these names choose to be discreet, to use them anonymously, or under the cover of some authority, who frequently happens to be as reliable as those I have cited. The facts justify the statement that today we are fairly agreed on the use of the units between the species and the genus, but as yet very much at sea in the use of those below the species (especially if typical) and above the genus.

Under the current Rules, the rank of a subtribe, tribe, subfamily and family is automatically determined by the ending, whether *-inae*, *-cae*, *-oideae*, or *-aceae*. This standardization has obvious advantages, but is not free from unwelcome results in practice. What is to be done with a name, legitimate in its ending for a certain rank, which has been erroneously placed as to rank by its author at publication? For example: Mueller Argoviensis

<sup>15</sup> This strange belief, for all I know, might hark back to a distinction which, apparently current before 1737, can be traced to the pages of Linnaeus' *Critica Botanica*. In this work, the names of Classes and Orders (modern Orders and Families) are said to be *muta* (silent), while those of Genera, Species, and Varieties are described as *sonora* (loud) (op. cit. 6; Phil. Bot. 158. 1751). That this distinction is academic can readily be seen, where Linnaeus states (op. cit. 138; Phil. Bot. 199. 1751) that the names of Classes and Orders have identically the same status as those of Genera. Beliefs rooted in custom die very hard; it may be suspected that a great deal of the current lack of feeling for trinomials, and many "philosophical" discussions about the use of subspecies and variety stem from thought once accepted in the American Code of 1904, and since dead in appearance rather than in fact.

published the *Pereae* as a subtribe. Subtribes must end in *-inae*, hence Mueller's name is now untenable in the subtribal rank. This name, on the other hand, is tenable for a tribe, for it ends in a legitimate manner in *-eae*. *Shall we honor the ending of the name in preference to its originally designated rank, or the other way around?* Shall we accept the *Pereae* of Mueller as good for a tribe because the name ends in *-eae*, or shall we reject it, because Mueller definitely intended it to stand at publication for a subtribe? As a third possibility, shall we undertake to correct the *Pereae* of Mueller, having this name read *Perinae*, still crediting the authorship to him with reference to the original publication?

The Rules do not provide a direct answer to these questions. Although I have ventured my opinion on them in the footnote of a previous paper (*Ann. Mo. Bot. Gard.* **29**: 355. 1942), I feel that a full discussion of the matter is still in order, and that some data may properly be contributed here on the score.

Whether corrections are acceptable, to have names like Mueller's *Pereae* turned into *Perinae*, with reference to the original publication and Mueller's authorship unchanged, seems to me to be a matter still subject to personal preferences. As such, this matter can be settled only by a free vote in Congress. The principle it involves—I should like to point out—is important, nevertheless, and not to be tampered with lightly.

The current Rules frown upon corrections which are not absolutely required by previous patent errors or misprints (Art. 59, 70, 71), and if modifications of the kind now under discussion are to be allowed, suitable modifications will have to be introduced in the Articles in question. Authors careful of the integrity of original citation, moreover, may not be inclined to alter names, crediting them to authors who never coined them as a straight matter of record. My feeling is that if anything must stand corrected, it is better to correct the rank, leaving the name itself unchanged, for it is to the name sooner than to the rank that the author's name is immediately attached. Corrections restricted to the rank, at any rate, will not lay hands upon the generalities now in the Rules about what may be corrected, and how. This, in my opinion, is a paramount consideration.

Considering that one of the fundamental Articles (Art. 4) requires that useless names be not published, and that names and forms be rejected which may cause confusion and error, I believe that by far the best possible solution is to accept, for instance, Mueller's *Pereae* as a tribe, disregarding Mueller's own designation of it as a subtribe. By so doing, we avoid publishing once again the *Pereae* and placing the original Muellerian entity of the same name in the synonymy of the subtribe *Perinae*. The simplification in reference and citation attending this procedure is patent. It may be feared by some that the honoring of names *on their endings*, that is, accepting

Mueller's Pereaee as a tribe, may lead to numerous nomenclatural changes. The danger, in my opinion, is not great: we merely shall accept the Pereaee Muell. Arg. (1866) in place of the Pereaee Pax & Hoffm. (1931). Authorships, consequently, are apt to be involved sooner than anything else. Few will be the cases in which the name itself will undergo a change, as when, for instance, the Tithymaloideae Vent. (1799), takes the place of the Crotonoideae Pax (1890). Naturally, when using a name published by an earlier author with a change of rank it will be necessary to acknowledge the fact for the sake of a full and correct citation. This can easily be done by following Tithymaloideae Vent., used as a subfamiliar name, with a standard abbreviation, such as p.o. (*pro ordine*). Changes in the names of families are now almost impossible, for, as it is well known, we are bound by a list of *nomina familiarum conservanda* (Syn. Propos. Nomencl. Sixth Intern. Bot. Congr. 64. 1935; Proc. Sixth Intern. Bot. Congr. 1: 358. 1936). The omissions in this list (Aizoaceae or Mesembryanthemaceae, for instance) may readily be remedied.<sup>16</sup>

Names originally proposed in the forms of a language which is neither Latin nor Greek are another source of confusion. Article 7 in the Rules which is supposed to speak in the matter, and is often referred to in discussion, is ambiguous. It reads: "Scientific names of all groups are usually taken from Latin or Greek. When taken from any language other than Latin, or formed in an arbitrary manner, they are treated as if they were Latin. Latin terminations should be used so far as possible for new names." This Article gives no examples, but refers, if I am not mistaken, to such names as *Macaranga* and *Ouratea*, *Schinus Molle* and *Quercus Tozza*, which, although neither Latin nor Greek in origin are to be treated as if they were of the classic languages. It cannot be construed to legitimize and protect such names as Périidées of Baillon, even less Luxembourgiés of Van Tieghem, because, unlike Baillon, Van Tieghem made it a point not to use Latin endings, setting his own standards up in defiance of those of every other botanist. It is patent, moreover, that Périidées does not end in *-cae*, and this automatically makes it illegitimate under Art. 24.

Granted that Art. 7 requires elucidation and proper restating, it may well be that the best way out of the difficulties created by the presence of names in the taxonomic record with French, German, and other such endings, which conflict with Art. 23 and 24, consists in a legitimization of current usage. Current usage undoubtedly tends to honor these names, so long

<sup>16</sup> Sprague's discussion (Jour. Bot. 60: 69. 1922) is probably the reason why the most important of these names have been omitted from this list. I firmly believe that Sprague's contentions are ill digested and disturbing to sound nomenclature. The influence which they have exerted will not long be hidden from a thoughtful reader of the notes of Melchior (E. & P. Nat. Pfl. 21: 109, footnote. 1925) and Krause (op. cit. 15(a) 224, footnote 2. 1930). Although Melchior agrees with Sprague, and Krause dissents, all these authors act with a full disregard of the existing rules of nomenclature.

as they have been published with a description and have priority. The Actinidiacées of Van Tieghem, for instance, (Jour. de Bot. **13**: 173. 1899) have been indorsed as Actinidiaceae by Gilg & Werdermann (in Engl. & Prantl, Nat. Pflanzenf. ed. 2 **21**: 36. 1925) and Rehder (Man. Cult. Trees Shr. ed. 2. 630. 1940).

Failure to accept these names as if published in the proper Latin form may ease the solution of some nomenclatural problems, but is certainly bound to complicate the definition of others, possibly more important. The list of the *nomina familiarum conservanda* in vigor insures taxonomy against unwelcome changes in the major units of classification, and a simplification in nomenclature is always most desirable. Accordingly, an addition should be made to Art. 23 and 24 to state that names above the genus are to be honored (if otherwise validly and legitimately published) which bear endings in French, German, or other modern languages, readily assimilable to the correct Latin forms *-inae*, *-cae*, *-oidcae*, and *-accæe*. The wording of such an addition is difficult. Formal proposals will be made in the future, if possible, in order to cover the changes suggested as needed in this study.

#### SUMMARY

This study consists of two parts, as follows:

(A) An historical review of the fundamental literature between the years 1735 and 1789, in which artificial and natural classification were at last clearly understood, and ultimately separated. Additional data are offered for the period between 1789 and 1905. The following works and dates are suggested as crucial, (1) Linnaeus' *Systema Naturae*, 1735; *Methodus Sexualis*, 1737; *Classes Plantarum*, 1738; (2) Adanson's *Familles des Plantes*, 1763; (3) Lamarck's *Flore Française*, 1778; (4) Antoine Laurent de Jussieu's *Genera Plantarum*, 1789. The revitalizing influence upon systematic thought of Bernard de Jussieu, who, although publishing nothing in botany, laid out in 1759 the plants of the garden of the Trianon according to the natural method of classification is underscored. Comments are specifically offered upon the works of Gleditsch, 1764; Haller, 1768; Necker, 1790; Ventenat, 1799; Jaume-St. Hilaire, 1805; A. P. De Candolle, 1805.

(B) A consideration of issues of practical nomenclature in the units above the genus. Doubts and confusions now prevailing in the handling of these units are pointed out. It is suggested that names published between the genus and the class be honored on their endings, disregarding, if necessary, the original designation of rank, and that names of the same nature published with formally improper endings in languages other than Latin be legitimized.

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EFFECT OF COTTON ON THE GERMINATION  
OF PHYCOMYCES SPORES<sup>1</sup>

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In earlier studies in this laboratory (2, 3, 4, 5) on the germination of spores of *Phycomyces blakesleeanus* a drop of a spore suspension was placed on an agar medium in a Petri dish measuring 15 × 100 mm. Each dish contained 10 ml. of the agar medium. After from 3 to 18 hours incubation, depending on the rapidity of germination, spore counts were made under the low power of a compound microscope. This method of studying the effect of various substances on spore germination has certain advantages. The spores are held in position on the agar medium; complete sterility, if desirable, is easy to maintain; the spores are exposed to the air; the dishes are convenient to handle. It has certain disadvantages also. The agar used should be especially purified (6) and it could perhaps interfere by adsorption or otherwise with the activity of some types of substances which are under investigation. If many substances and concentrations are studied the space occupied by the dishes becomes a factor to be considered. Furthermore, the 10 ml. of medium used in a dish requires more material than is desirable if the substance to be tested is available in limited amounts. Smaller Petri dishes measuring 15 × 60 mm. and containing 2.5 ml. of medium solidified on one side of the dish were substituted for the larger ones with satisfactory results.

**Use of 1 ml. of Medium in Spot Plates.** More recently use has been made of Pyrex plates, 85 × 100 mm. in size, with 9 concave depressions, 22 mm. in diameter and 7 mm. deep (fig. 1). These depressions conveniently hold 1 ml. of medium and it is possible to run nine different media on a single plate. This method has all the advantages of an agar medium in a Petri dish and is economical of space and material. The procedure in our experiments was as follows:

The basal agar medium consisting per liter of 1.5 g.  $\text{KH}_2\text{PO}_4$ , 0.5 g.  $\text{MgSO}_4 \cdot 7 \text{H}_2\text{O}$ , 50 g. dextrose, 1.0 g. asparagine, 500  $\mu\text{m}$  moles thiamine, and 10 g. purified agar<sup>2</sup> was sterilized in 10-ml. quantities in a 20 × 150-mm. test tube, tube (A) in figure 2. The supplements whose effect on germination was to be studied were sterilized in about 0.2 ml. of distilled water in a test tube,

<sup>1</sup> This research was supported in part by Mr. Manfred Wahl, whose kindly and intelligent interest the authors are pleased to acknowledge.

<sup>2</sup> To this the following mineral supplements in p.p.m. were added: 0.005 B, 0.02 Cu, 0.10 Fe, 0.01 Ga, 0.01 Mn, 0.01 Mo, and 0.09 Zn.

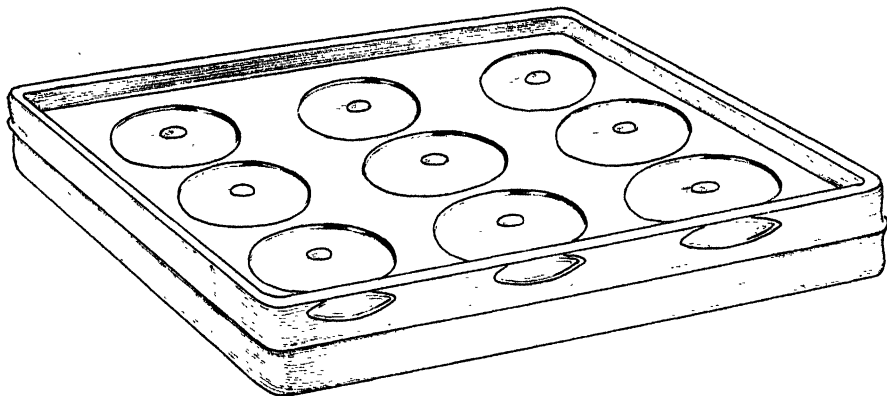


FIG. 1. Pyrex spot plate. Each depression contains 1 ml. of an agar medium, and one drop of spore suspension has been placed on each spot.

tube (B) in figure 2. After sterilization 1 ml. of the melted basal agar medium from (A) was added with a sterile pipette to the 0.2 ml. of liquid containing the supplement in (B). After mixing, the agar was poured into a depression in the plate which had been previously sterilized. If no supplement was used the basal medium was mixed with 0.2 ml. of distilled water separately sterilized in (B). When the agar had solidified in the depression a drop of spore suspension in sterile distilled water was placed on the surface of the agar by means of a platinum loop about 3 mm. in diameter. The inoculated plates (fig. 1) were piled one on another, the top one covered with a piece of glass or an empty plate, and placed in a moist chamber for incubation at from 25° to 26° C. Eight hours were selected as a convenient and satisfactory time for incubation. At the end of that time the plates were set in a refrigerator and held until the next day for counting.

**Results with Hypoxanthine and a D<sub>r</sub> Fraction.** When this method<sup>3</sup> was used, *Phycomyces* spores from cultures from 6 to 9 days old showed 1 per cent germination or less on the basal medium. The addition of hypoxanthine or of a D<sub>r</sub> fraction prepared from potato<sup>4</sup> increased the germination slightly. However, hypoxanthine and the D<sub>r</sub> fraction together had a marked effect (table 1). In the presence of 5.0 mg. of the D<sub>r</sub> fraction the activity of 0.1 mμ mole (0.0136 μg.) of hypoxanthine could be observed. The effect of the hypoxanthine increased up to 50 mμ moles per ml. and decreased with larger amounts.

Although the results within a single experiment were consistent the per cent germination for a particular combination of hypoxanthine and the D<sub>r</sub> fraction was not duplicated in successive experiments. For example, when

<sup>3</sup> Absorbent cotton was used for plugging the tubes in these experiments. See later discussion.

<sup>4</sup> The preparation of this fraction is described by Robbins and Hamner (4).

TABLE 1. *Effect of hypoxanthine and a D<sub>r</sub> fraction from potato on germination of Phycomyces spores*

	No addition	0.5 mμ mole hypoxanthine	5.0 mμ moles hypoxanthine	5.0 mg. D <sub>r</sub>	0.1 mμ mole H + D <sub>r</sub>	0.5 mμ mole H + D <sub>r</sub>	1.0 mμ mole H + D <sub>r</sub>	5.0 mμ mole H + D <sub>r</sub>	10.0 mμ mole H + D <sub>r</sub>	50.0 mμ mole H + D <sub>r</sub>	100.0 mμ mole H + D <sub>r</sub>	1000.0 mμ mole H + D <sub>r</sub>
Exp. 1 .....	1	.....	4	5	9	15	28	..	58	63	53	22
Exp. 2 .....	1	.....	4	8	23	31	31	..	80	83	78	.....
Exp. 3 .....	1	2	3	8	14	28	47	68	....	..	..	..
Exp. 4 .....	<1	1	3	3	20	41	54	87	..	..	..	....

1.0 mμ mole of hypoxanthine and 5.0 mg. of the D<sub>r</sub> fraction per ml. were used the per cent germination varied in four successive experiments from 28 to 54. We are unable to account for this variation. The per cent germina-

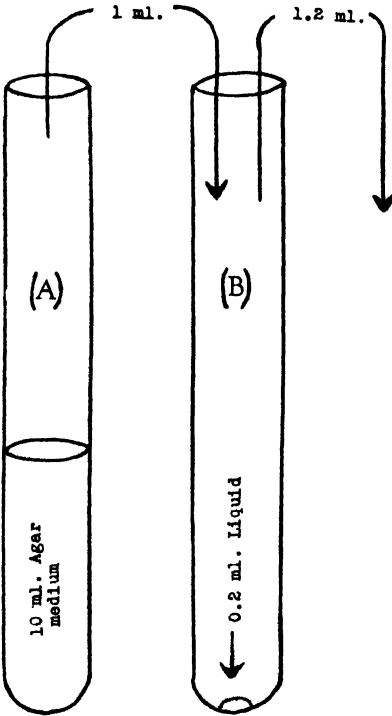


FIG. 2. For explanation see text.

tion is affected by the age of spores, temperature of incubation, and time of incubation as well as by the composition of the medium, but we were not able to select any variable which could account for the differences between experiments to which attention has been called.

**Effect of Cotton Plugs.** However, an inconsistency in one of our experiments led to the discovery that under certain conditions the cotton used in plugging the test tubes materially influenced the results. Since this observation may be of more general interest than for the study of the germination of *Phycomyces* spores it seemed worth while to report our results.

The experiment which led to this discovery was as follows:

Certain supplements whose effect was to be studied were used with the basal agar medium containing 5  $\mu$  moles of hypoxanthine per ml. In some instances the supplements were autoclaved in 0.1 or 0.2 ml. of distilled water in test tubes (B) plugged with ordinary cotton. One ml. of the agar medium from tube (A) containing 10 ml. was added to the small amount of liquid containing the supplements in tube (B) and the mixture poured into a depression in the plate. The germination ranged from 16 to 44 per cent. In other instances the supplements were sterilized in 10 or 15 ml. of distilled water and 0.1 or 0.2 ml. of this liquid were mixed with 1 ml. of the agar medium in an empty dry sterile tube before it was poured into the depression in the plate. The germination ranged from 2 to 5 per cent. It appeared therefore that beneficial material was extracted from the walls of the test tube or from the cotton plug of tube (B). When all the active material obtained from a test tube was added to 1 ml. of medium the beneficial effect on germination was marked. When one-fiftieth or less of the extract from a test tube was included with 1 ml. of medium, as occurred when the supplements were sterilized in 10 or 15 ml. of distilled water, the effect was negligible.

**Effect of Glass of Test Tube.** We first suspected that something might have been dissolved from the glass of the test tubes during autoclaving. Since the test tubes were cleaned with chromic acid-sulfuric acid cleaning mixture, we thought traces of chromic acid left in the tubes were removed by autoclaving and concentrated in the small amount of liquid in the bottom of tube (B). New test tubes were rinsed with distilled water, 0.1 ml. or 0.2 ml. of distilled water were added to each tube, the tubes were plugged with ordinary cotton and autoclaved. The same procedure was followed with old tubes which had been cleaned with chromic acid cleaning mixture. After autoclaving some of the old tubes were rinsed with distilled water, 0.1 ml. or 0.2 ml. of distilled water were placed in each tube, the old plugs were replaced and the tubes resterilized. One ml. of agar medium from a 10 ml. quantity was added to each tube. In one set of experiments the basal medium was used and in another the basal medium plus 5.0  $\mu$  moles of hypoxanthine per ml.

Both old and new test tubes yielded extracts which were beneficial with the agar medium containing hypoxanthine (table 2). The tubes autoclaved twice with rinsings between autoclavings yielded extracts distinctly beneficial though less so than those autoclaved once. The extracts were ineffective

TABLE 2. *Per cent spore germination when media given were mixed with distilled water autoclaved in test tubes stoppered with cotton*

	Basal medium tube (A)		Basal medium plus 5.0 m $\mu$ moles hypoxanthine per ml. in tube (A)	
	0.1 ml. distilled water in tube (B)	0.2 ml. distilled water in tube (B)	0.1 ml. distilled water in tube (B)	0.2 ml. distilled water in tube (B)
New test tubes .....	4	3	30	30
Old test tubes .....	4	2	33	38
Old tubes autoclaved twice with rinsing between .....	3	2	20	18

in the basal medium without hypoxanthine and it appeared immaterial whether the quantity of liquid autoclaved in tube (B) was 0.1 or 0.2 ml.

**Effect of Various Kinds of Cotton.** Since little difference was observed between the effect of old or new tubes an experiment was performed in which the tubes (A) containing the agar medium (basal medium plus 5.0 m $\mu$  moles hypoxanthine per ml.) were sterilized without plugs, with plugs of ordinary cotton, or with plugs of absorbent cotton. The tubes (B) containing 0.2 ml. of distilled water also were autoclaved open, plugged with ordinary cotton or plugged with absorbent cotton. No difference was noted between the open tubes containing 10 ml. of the agar medium and those plugged with cotton. Whenever tubes (B), containing the 0.2 ml. of distilled water, were plugged with ordinary cotton the per cent germination was high (table 3). It appeared, therefore, that material beneficial to spore germination was extracted in autoclaving a test tube plugged with ordinary cotton batting. One-tenth of the material extracted from a single plug was ineffective. This conclusion followed because 1 ml. of the 10 ml. of basal medium from tubes A plugged with ordinary cotton was inactive. The material was not extracted from plugs of absorbent cotton.

TABLE 3. *Effect of autoclaving open tubes or plugged tubes on per cent germination of Phycomyces spores*

Tubes (A) of basal medium autoclaved	Tubes (B) with 0.2 ml. distilled water autoclaved	Per cent germination
Open	Open	5
Open	Plugged ordinary cotton	55
Open	Plugged absorbent cotton	5
Plugged ordinary cotton	Open	4
Plugged ordinary cotton	Plugged ordinary cotton	54
Plugged ordinary cotton	Plugged absorbent cotton	6
Plugged absorbent cotton	Open	5
Plugged absorbent cotton	Plugged ordinary cotton	42 +
Plugged absorbent cotton	Plugged absorbent cotton	7

Further experiments showed that the beneficial material was extracted under the conditions given above from freshly ginned cotton, from "sanitary" cotton, but not from "aseptic non-absorbent" cotton.<sup>5</sup> We found also that it was not always necessary to use a small amount of liquid in the test tube (B) during autoclaving. Sufficient water of condensation was sometimes formed during autoclaving an empty tube plugged with cotton so that the beneficial effect could be observed after the basal medium had been added to such a tube.

**Location of the Beneficial Material in the Test Tube.** Since the 1 ml. of agar medium was added to a test tube (B) containing 0.2 ml. of liquid and then poured into a depression in the Pyrex plate it appeared possible that the beneficial material might have come either from the small amount of liquid in the bottom of a tube (B) or from the lip of the tube which was in contact with the cotton during autoclaving. Our experiments showed that the beneficial material was in the liquid and did not come from the lip of the tube. This was demonstrated by autoclaving 0.2 ml. of distilled water in open tubes or in tubes plugged with ordinary cotton. The basal agar medium plus 5.0 m $\mu$  moles of hypoxanthine per ml. was added to both types of tubes. The agar from one set of tubes (B) plugged before autoclaving was poured into the depressions in a Pyrex plate so that it ran over the lips of the tubes. The agar from another set was removed with a pipette and had no contact with the lips of the tube. The per cent germination for the agar prepared with the open tube was 2; for the agar poured out over the lip was 34; and for that removed with a pipette, 33.

**Source of the Beneficial Material.** It was noted that the small amount of liquid in a stoppered tube usually contained a few strands of cotton which fell from the cotton plug. It was found, however, that these strands were not responsible for the beneficial material which was apparently distilled by steam from the plug into the tube during autoclaving. This was demonstrated by comparing the activity after autoclaving of tubes (B) plugged in the customary way with cotton, open tubes in which a few strands of cotton were placed in the 0.2 ml. of distilled water in the bottom of the tube, and tubes stoppered with plugs wrapped with cheese cloth which had been thoroughly washed. The liquid from the open tubes in which a few strands of cotton had been placed was not active, and that from tubes plugged with the wrapped plugs was nearly as effective as that from the tubes plugged in the ordinary way.

<sup>5</sup> The sanitary cotton is described by the manufacturer as thoroughly washed, free of black specks and lint; a good grade of cotton for routine bacteriological work.

The aseptic non-absorbent cotton is described as absolutely sterile, a high-grade material used for plugging bacteriological apparatus.

The assumption that the active material was steam-distilled from the cotton plug was confirmed by the following experiment. About 3.0 g. of air-dry cotton were placed in a condenser. Dry steam passed up through the cotton was condensed and collected. During the distillation steam was run through the jacket of the condenser containing the cotton so that the current of steam passing through the cotton did not condense. Used with the basal medium plus 5  $\mu$  moles hypoxanthine per ml., a 0.2-ml. portion of the first part of the distillate consisting of 8 ml. gave 20 per cent germination, as compared to 5 per cent without the extract, 0.2 ml. of the second portion (3.5 ml.) of the distillate gave 9 per cent, and 0.2 ml. of a third portion (1 ml.) 7 per cent. The per cent germination obtained with the liquid in a plugged tube containing 0.2 ml. of distilled water was 27. It appeared from this experiment that the active material was volatile with steam and that most of it was extracted from 3 g. of cotton in the first 8 ml. of distillate. The 8 ml. in the first distillate was obtained from 3 g. of cotton and 0.2 ml. was tested. Therefore, the extract of about 0.07 g. of cotton obtained in this way favorably affected the germination of *Phycomyces* spores. The distillate was water-clear and had a pH of 3.9.

**Additional Observations on the Active Material.** Further experiments which will not be detailed here demonstrated the following: No active material was observed in the distillate when 100 g. of moist cotton were placed in a flask with 100 ml. of distilled water and the water was partially distilled by heating the flask in a bath of saturated NaCl. Moist cotton dried at 100° C was still active. The active material was not destroyed or driven off by heating dry cotton at 50° or 100° C for 7 days. An active solution was obtained by autoclaving at 14 lbs. for 1 hour an 8-quart stainless-steel kettle containing 58 ml. of distilled water and plugged with 580 g. of cotton. The extract was water-clear and had a pH of 5.0. In the basal medium, on which 2 per cent germination was observed, 0.1 ml. of this extract (equivalent to 1.0 g. of cotton) gave 25 per cent and 0.2 ml., 46 per cent germination. The active material was not lost when a solution was evaporated to 1/100 its original volume. It disappeared when dried over night (about 18 hrs.) at 50° C or for 2½ hours at 100° C. Most of the activity disappeared with 45 minutes drying at 100° C. When an active extract was neutralized with NaOH and dried at 50° or 100° C over night, most of the activity remained.

Attempts to determine dry matter of the unneutralized extract were unsuccessful. For the neutralized extract from tubes plugged with cotton we found the extract from 1 g. cotton contained 0.034 mg. of dry matter. The extract obtained with the stainless steel kettle contained 0.017 mg. of dry matter per g. of cotton.

**Active Material Compared to Hypoxanthine and D<sub>r</sub> Fraction.** The material extracted from the cotton plugs appeared to contain little or no

hypoxanthine or a substitute therefor. It acted in part like the  $Z_2$  factor (contained in the  $D_r$  fraction from potato tubers). This is indicated by its inactivity<sup>6</sup> in the basal medium lacking hypoxanthine (tables 2, 4) and relative ineffectiveness in the basal medium supplemented with the  $D_r$  fraction only (table 4). The extract from a single plug in a test tube containing 0.2 ml. of distilled water was more effective on germination than 0.5 mg. of the  $D_r$  fraction and less effective than 5 mg. of the  $D_r$  fraction. This conclusion follows by comparing the germination obtained with a plugged tube (B) on a medium containing 5  $m\mu$  moles of hypoxanthine (51%) with that obtained with open tubes (B) on a medium containing 5  $m\mu$  moles of hypoxanthine and 0.5 mg. of the  $D_r$  fraction (31%) and that containing 5  $m\mu$  moles of hypoxanthine and 5 mg. of the  $D_r$  fraction (65%).

Table 4. *The effect of cotton plugs in tube (B) compared with no plugs on germination of Phycomyces spores on basal medium plus supplements as given*

	None	1 $m\mu$ mole hypo- xanthine	5 $m\mu$ moles hypo- xanthine	0.5 mg. $D_r$ fraction	5 mg. $D_r$ fraction	1 $m\mu$ mole hypo- xanthine plus 0.5 mg. $D_r$ fraction	5 $m\mu$ mole hypo- xanthine plus 0.5 mg. $D_r$ fraction	1 $m\mu$ mole hypo- xanthine plus 5 mg. $D_r$ fraction	5 $m\mu$ moles hypo- xanthine plus 5 mg. $D_r$ fraction
No plug . . . . .	1	2	5	2	12	11	31	65	79
Plug . . . . .	2	17	51	4	20	39	74	70	89

The active material obtained with dry steam from cotton differs from the  $D_r$  fraction in having little effect on the growth of the germ tubes. Its action was limited to increasing the germination. It cannot, therefore, be considered to be equivalent to the  $D_r$  fraction except in its effect on spore germination.

**Active Material Considered as an Organic Acid.** The properties of the active material suggest that it is an organic acid perhaps adsorbed by the cotton and freed from it by dry steam. The active extracts from cotton were slightly acid; the active material could be concentrated by evaporation but was volatile on drying at 50° or 100° C unless neutralized. These characteristics would agree with those of an organic acid.

Furthermore, organic acids beneficially affect the germination of *Phycomyces* spores as has been previously reported from this laboratory (5) and the effective quantity of propionic acid (and perhaps acetic acid) was found to be of the same order of magnitude as the dry matter determined in active extracts of cotton studied in this paper. Although it required 1 mg. of sodium

<sup>6</sup> The extract increased the per cent germination in the absence of hypoxanthine if used in amounts equivalent to 10 g. or more of cotton.



acetate in the basal medium to produce the same effect as the extract from a cotton plug (about 1.0 g. of cotton) in the presence of hypoxanthine the quantity of acetate necessary was between 0.025 and 0.050 mg. Sodium propionate was more effective than sodium acetate (table 5). One mg. of the propionate in the basal medium was more effective than the extract from a cotton plug and in the presence of hypoxanthine the quantity of propionate required was between 0.005 mg. and 0.010 mg. We found 0.034 mg. of dry matter per plug in the extract obtained from plugged tubes and 0.017 mg. per g. of cotton in the extract obtained with the steel kettle. These figures are in the same class with the amounts of propionate and acetate active in affecting the germination of spores of *Phycomyces*.

TABLE 5. *Per cent germination of Phycomyces spores in the presence of various amounts sodium acetate or sodium propionate in the basal medium and the basal medium plus 5  $\mu$  moles of hypoxanthine per ml.*

Mg. of sodium salt per ml. medium	Na acetate	Na acetate and 5 $\mu$ moles hypoxanthine	Na propionate	Na propionate and 5 $\mu$ moles hypoxanthine
1.000	25	92	55	98
0.050	< 1	36	2	85
0.025	< 1	12	2	75
0.010	< 1	7	1	44
0.005	< 1	2	1	16
0.000	< 1	1	< 1	1
Plugged tube	...	28		28

It should be added that both the cotton extracts and the organic acids had little influence on growth and the activity of each was greater in the presence of hypoxanthine than in its absence.

#### DISCUSSION

We have previously reported (6) that thiamine, biotin, and pyridoxine are present in cotton and may be extracted in amounts sufficient to affect the growth of microorganisms if, during autoclaving, water of condensation drips through the plugs into the medium. This rarely occurs and may readily be observed by noting whether the plugs are wet or dry after autoclaving. In the experiments reported here the active material was extracted by the steam in the autoclave; no liquid passed through the cotton plugs, which were entirely dry after autoclaving. This source of growth-promoting material is of no significance in many experiments but it may be a serious source of error in others.

In our experiments plugs made of absorbent cotton or of aseptic non-absorbent cotton did not yield sufficient material to influence the response we were studying and one-tenth of the quantity obtained during autoclaving

from a plug of ordinary cotton was below the limit of activity detectable by our methods.

In studies of the sporogenous growth factor Knight and Fildes, in a paper quoted by Knight (1), found it necessary to wrap the cotton wool plugs in washed gauze to prevent cotton fibers dropping into the culture medium, which would have given sufficient contamination of active substance from the fibers to vitiate the experiment. Wrapping the plugs in our experiments did not prevent active material entering our culture media as we prepared it. Sherwood and Singer (7) found folic acid to be present in cotton and they suspected cotton plugs to be a source of error in their experiments.

Our observations and those of others emphasize the necessity of considering in any experiments with microorganisms the role that cotton may play and of making certain by appropriate means that substances derived from the cotton used in stoppering the apparatus are not a complicating factor.

#### SUMMARY

A method of studying the germination of spores of *Phycomyces blakesleeanus* using 1 ml. of agar medium in spot plates of Pyrex glass is described. Extracts favorably affecting spore germination were obtained by autoclaving cotton-plugged tubes. The active material was distilled from the cotton plugs by dry steam. It was not removed by heating moist or dry cotton at 100° C. It was thermostable and could be concentrated in water solution by evaporation. It disappeared on drying an active solution at 50° or 100° C unless the solution was neutralized. It is believed to be an organic acid adsorbed by the cotton and freed by dry steam.

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## A MORPHOLOGICAL AND CYTOLOGICAL STUDY OF A NEW FORM OF *VOLVOX*—I\*

JEROME METZNER

### INTRODUCTION

Although *Volvox* has been investigated frequently since its discovery by Leeuwenhoek (1700), many gaps in our knowledge of it remain. The need for extended comparative studies, especially of living material, has been emphasized by Pascher (1927), who maintains that a thorough and exact observation of the *Volvox* forms of different countries must be preliminary to monographic treatment of the genus. In addition, Pascher concludes that even the European species of *Volvox* have been described unsatisfactorily.

Few investigations have been made on American species of *Volvox* since the pioneer work of Powers (1907, 1908). Pocock (1933a, b), however, has illustrated the morphology and life history of South African species with unusually clear photographs and descriptions of living material. The only detailed account of mitosis and meiosis in *Volvox* is that of Zimmerman (1921) on *Volvox aureus*. Because division figures even in abundant material are difficult to find, this aspect of research on *Volvox* has been neglected.

The organism—*Volvox Carteri*—considered in this paper has been reported by five other workers, Powers (1908), Shaw (1922c), Iyengar (1933), Playfair (1918), and Apte (1936), from widely separated parts of the world since its original description by Carter (1859) from Bombay, India. These reports are limited to the more obvious details of morphology.

### METHODS

The morphological aspects of this paper are based primarily on detailed observations of living material. The abundance of *Volvox Carteri* permitted observations over long periods. Temperature and pH determinations were made at the source from time to time, and various other ecological factors were noted. The organisms were concentrated by means of a small plankton net. Water draining from the net was collected in large glass jars into which *Volvox* colonies were later introduced. Some of the concentrated *Volvox*

\* The second part of this study, containing the cytological and taxonomic portions, will appear in a subsequent issue of the Bulletin. All the figures for both parts appear with part I. The list of literature cited in both parts will appear with part II.

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material was fixed at the time of collection, and some subsequently at hourly intervals in Flemming's weak solution, Iodine-formalin solution (Johansen 1940), Chrom-acetic solution, Allen's B15 solution, and Navaschin's fluid. For cytological study, Flemming's solution gave the best results. All processes up to sectioning were carried on in shell vials which were ultimately broken to release the imbedded material. Sections were cut 5  $\mu$ , 7  $\mu$ , 10  $\mu$  and 12  $\mu$  thick, and these were stained in the following solutions: Heidenhain's iron-alum haematoxylin, Flemming's triple stain, Newton's gentian violet, Safranin, and the Feulgen stain. Of these, a short method employing Heidenhain's iron-alum haematoxylin gave the best results in general. Newton's gentian violet was excellent for revealing the structure of the pyrenoids, but it was ineffective as a nuclear stain. The Feulgen nuclear reaction was especially helpful in tracing changes occurring within the nucleus during the mitotic cycle, and served to confirm the mitotic picture observed after staining with Heidenhain's iron-alum haematoxylin. Fast green was used as a counter-stain.

Oospores in various stages of development were picked up with a fine pipette and placed in a small slot cut into a jelled agar plate. Fixative was added (usually Flemming's weak) and the slot was sealed by pouring molten agar over it. After this had jelled, a small agar cube containing the fixed oospores was cut out of the plate and placed into a vial containing fixative. Subsequently, the agar blocks were treated as were the *Volvox* colonies described above. Because oospores contain much stored food material, they blacken considerably after Flemming fixation. Prolonged bleaching in  $H_2O_2$  or chlorine water was therefore employed.

Membrane studies were made on living colonies treated with dilute methylene blue, according to the method of Meyer (1896), and also on stained, microtomed sections.

#### ECOLOGICAL DATA

*Volvox* was found abundantly in large tanks<sup>1</sup> approximately 15 feet long, 5 feet wide, and 1 foot deep containing pond lilies, and less frequently in those in which *Sagittaria*, *Lotus*, or *Pistia stratiotes* was growing. As might be expected, the amount of *Volvox* available at any given time varied considerably from tank to tank. In some, growth was so rich that the water looked green, whereas others nearby contained relatively few colonies. Varying conditions within the tanks were responsible for differences in growth rates and cycles. Changing of the seed plants in the tanks, changes of water, disinfections and removal of algae such as *Hydrodictyon* probably affected the growth of *Volvox*.

<sup>1</sup> I am grateful to William Tricker Inc. for generous consideration in permitting me to have free access to tanks located at Saddle River, Bergen County, New Jersey.

*Volvox* occurred in water ranging in temperature from 27° to 33° C, but most often at about 28°. These water temperature readings were taken at the surface. Readings taken at the bottom of the tanks were 5° to 9° C lower.

In bright sunlight the *Volvox* colonies exhibited a strong thigmotactic response to leaves and stems of the plants associated with it. Pond lilies or other plants were, at times, covered with dense green accumulations of colonies on the surfaces of the submerged parts. If the pond lilies were disturbed, the *Volvox* became free swimming but returned later to cover the leaves and stems.

The pH of water containing *Volvox Carteri* was fairly constant, ranging usually from 7.2 to 7.5.

#### CULTIVATION

Zimmerman (1921) kept *Volvox aureus* for three months and *Volvox globator* for ten months in 1-6-liter glass containers of source water covered up to the water line with black paper to prevent lateral illumination. Pocock (1933b) did not succeed in establishing vigorous permanent *Volvox* collections, and depended upon the abundant natural material available. Uspenski and Uspenskaja (1925) found that *V. minor* (*V. aureus*) and *V. globator* have a relatively high iron requirement, and devised a culture medium in which the organism could be maintained for prolonged periods. Other workers (Knoke 1924, Mainx 1929a, b, Pringsheim 1930, Lefèvre 1932) have reported techniques for the culture of *Volvox*. These contributions indicate that continuous cultivation of *Volvox* in the laboratory is difficult.

Culture experiments were attempted with the following types of solutions:

1. Uspenski's fluid (Uspenski and Uspenskaja 1925).
2. Bold's soil extract #2 (Bold 1936).
3. Source water.
4. Source water plus iron salts (0.5 mg.  $\text{Fe}_2\text{O}_3$  per liter).
5. Source water plus Uspenski solution (20%).
6. Source water plus Fe salts (0.5 mg.  $\text{Fe}_2\text{O}_3$  per liter) plus  $\text{KNO}_3$  (0.5 gm. per liter).
7. Uspenski solution with citrate buffer (potassium citrate added in concentration of 0.004 M per liter).
8. Moewus' solution (10%) (Moewus 1940).

At first, for each of these solutions three series were set up: (1) single asexual colonies in 25 ml. of solution, (2) 15-25 asexual colonies in 25 ml. of solution, (3) large numbers of all types of colonies in 100 ml. of each solution. From the initial experiments it was found that only solutions 1, 3, 5, and 8 were somewhat successful, and in these only the third series containing large initial numbers of *Volvox* managed to maintain themselves for any appreciable time. Best results were obtained from the use of Uspenski's solution full strength or a combination of source water and

Uspenski's solution (20%). During the latter part of July, August, and early September *Volvox* was maintained in these solutions in quart jars placed on the broad sill of an east window. Here cultures received direct sunlight only during the morning hours and indirect light the rest of the day. It was necessary to add some additional Uspenski's fluid (25-50 ml.) or a few drops of its component  $\text{FeSO}_4$  solution every week. When collections were left in their original source water, they soon degenerated. Apparently, therefore, species of *Volvox* differ in their ability to grow under laboratory conditions. Some, *V. aureus* and *V. globator*, persist for some time in source water (Zimmerman 1921); others, *V. Carteri*, *V. Rousseletii*, and *V. capensis*, perish within a few days (Pocock 1933b); the life of some species, *V. Carteri*, *V. minor*, and *V. globator*, is prolonged in culture by regular addition of iron salt (Uspenski & Uspenskaja 1925); light and temperature are also important factors. In spite of numerous experiments, it was not possible to maintain *V. Carteri* indefinitely in culture in the laboratory.

#### MORPHOLOGY AND LIFE HISTORY

The membrane structure of *V. Carteri* resembles to a remarkable degree that of *V. tertius* Meyer described by Pocock (1938) and is similar to that of *V. gigas* Pocock and *V. africanus* Rich & Pocock in general plan of structure.

A common colony membrane encloses the peripherally placed cells (figs. 37, 39). Directly outside the apex of each protoplast the common membrane is slightly depressed, and through the floor of this depression the two flagella project. Dilute methylene blue used on living material (fig. 97), as well as on paraffin sections, reveals the structure of the membrane and of the interior of the coenobium (fig. 92). Each protoplast occupies the outer portion of a pentagonal, hexagonal (most commonly), or heptagonal gelatinous prism with a dome-shaped outer membrane lying just below the common colony membrane (figs. 39, 41, 55). The prisms taper slightly toward their inner limits, which are bounded by slightly curved membranes. Gelatinous<sup>2</sup> material occupies the space between the dome-shaped membranes of the prisms and the periphery of the colony. Within each coenobium there is present a somewhat alveolated, amorphous gelatinous material denser near the prisms and much less dense or absent at the center. Each protoplast of reproductive cells is surrounded by a closely adhering cell membrane and is enclosed within a wide saccular vesicle formed by the enlarged prism membrane extending into the interior of the mother colony (figs. 51, 52). Pocock (1933a) states that in *V. gigas* "the cells of the young embryo are not enclosed in a common membrane" and

<sup>2</sup> The word gelatinous is used to indicate the physical rather than the chemical nature of this material.

mentions earlier in the same paper that the common envelope is formed after inversion. Her illustrations do not show a common colony membrane in pre-inversion daughters of *V. africanus*, but in her paper on *V. tertius* (1938) figure 2c shows what is apparently a common colony membrane in a daughter about to invert, although this structure is not mentioned in the textual discussion of this stage. In *V. Carteri* the common colony membrane (presumably derived from the cell membrane of the original gonidial protoplast) is clearly evident (fig. 92) even in the early stages of gonidial division. It is closely attached to the underlying cells, whereas the prism membrane, forming a wide vesicle around the developing daughter, extends into the interior of the mother coenobium, and is there limited by the internal gelatin or by vesicular membranes of developing sister colonies. After the gonidia sink beneath the surface of the parent colony, their gelatinous prisms swell to such an extent that their original polygonal shape is lost, and as the daughters develop within them, they enlarge and occupy almost all of the hollow central cavity of the parent colony.

Powers (1908), Iyengar (1933), and Apte (1936) noted that there is a gradual diminution from the anterior to the posterior pole of the colony in the distances between neighboring protoplasts in the forms of *V. Carteri* they observed. This is also evident in the organisms of the present study. The protoplasts at the anterior poles of the adult colonies are more widely separated than those at the posterior pole (figs. 94-96).

Because the coenobia are not exactly spherical, but somewhat ovoid, nor the protoplasts evenly spaced, estimations of cell members in colonies can be only coarse approximations. Janet's (1923a) method of squaring the number of cells counted on a great circle and then multiplying by 0.318 was used in estimating the number of cells in coenobia. There is some difficulty in counting accurately the cells in a great circle. Other methods have been used by Klein (1889a), Zimmerman (1921), and Shaw (1922b), but Janet's method seems to be simple and fairly accurate. A summary to be presented later includes data on cell numbers.

*Volvox* colonies contain, in general, two types of cells: (1) purely vegetative cells, (2) reproductive cells. The latter participate in reproductive processes in addition to carrying on all vegetative processes, with the exception of contributing to motility of the parent. The reproductive cells are sometimes interpreted as specialized cells, whereas they are really more primitive physiologically than the vegetative cells. They have retained their capacity to perform all fundamental life functions (with the exception of motility), including that of reproduction, whereas the purely vegetative cells have become specialized by losing their capacity to reproduce. In *Volvox* colonies, therefore, the majority of the cells are physiologically specialized and relatively few; the reproductive cells remain physiologically

primitive, but they have undergone morphological differentiation which adapts them to their special reproductive functions.

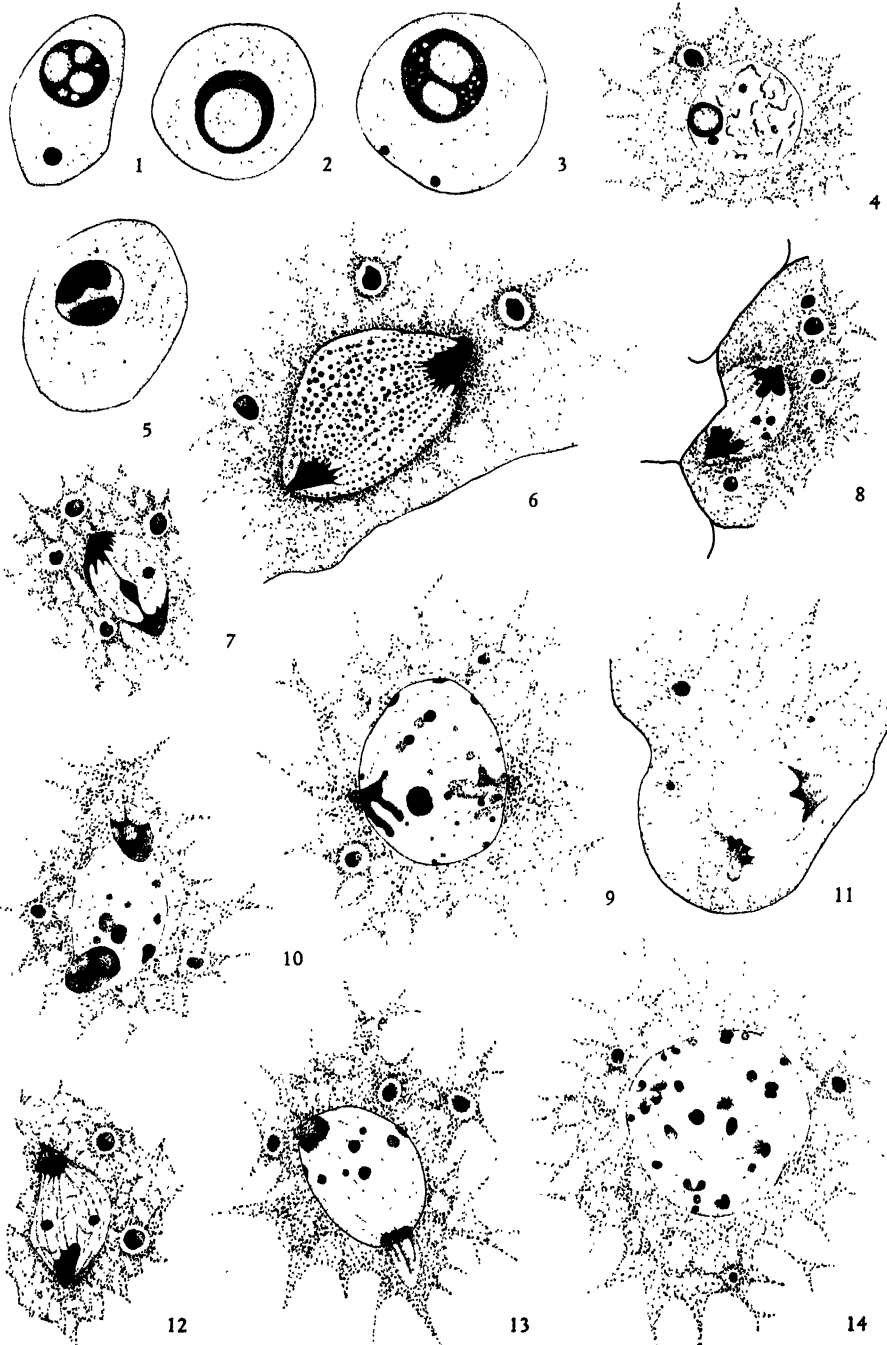
Protoplasts of purely vegetative cells are distinctly *Chlamydomonas*-like, and in adult colonies are not connected by protoplasmic strands. Each is contained within a gelatinous wall in the form of a polygonal prism bounded by membranes (figs. 37, 42, 56). A large cup- or bowl-shaped chloroplast occupies the base and sides of the protoplast, but does not extend completely to the apex, thus leaving a clear area. At the base of the chloroplast is a large pyrenoid (infrequently two) consisting of a spherical center surrounded by from two to six (usually four) starch plates (fig. 40). Figure 117 shows division of a pyrenoid. This would seem to indicate that pyrenoids arise from preexisting pyrenoids by division, but does not preclude the possibility that some arise *de novo* as various workers have reported (Overton 1889; Zimmerman 1921). Within the upper hollow portion of the chloroplast lies the nucleus ( $3-4\mu$ ) with its endosome prominent even in the living condition. Two separated flagella, from two and one-half to three times the length of the protoplast, arising from refringent granular blepharoplasts at the apex of the protoplast, project through the prism and common colony membrane to the exterior. Two contractile vacuoles, alternately expelling their contents, are also located in the colorless apex. The investigations of Mast (1907, 1919, 1922, 1926, 1928, 1932) have added much to our knowledge of the structure and function of the eyespot (stigma) in *Volvox* and related organisms. Pocock (1938) states that the stigma, in all species of *Volvox* as yet investigated, lies in the posterior prolongation of the chloroplast and is usually situated symmetrically in relation to the points of insertion of the two flagella. In the anterior polar region of the material here studied the stigma lies about a third of the length of the cell from its apex. As the distance from the anterior pole increases, the position of the stigma rises, while its size decreases, until at the equator of the colony the eyespot is reduced to a minute speck at the apex of the cell. In the posterior part of the colony there are no eyespots (figs. 94-96). One or more highly refractive bodies, vibrating back and forth in Brownian movement, frequently occur near the stigma (fig. 37). Pocock (1938) also found these in *V. tertius* and identified them as volutin.

In coenobia crushed by cover glass pressure certain vegetative cells at the torn portions of the colony frequently become free-swimming. Their resemblance to *Chlamydomonas* is remarkable. No attempt has been made, as yet, to culture these cells nor to study their subsequent behavior. It is unlikely that such a phenomenon would occur in species with protoplasmic connections.

#### REPRODUCTION

Three types of reproductive cells occur, each in a separate colony: (1) Gonidia (daughter colony initials) which form daughter colonies by divi-





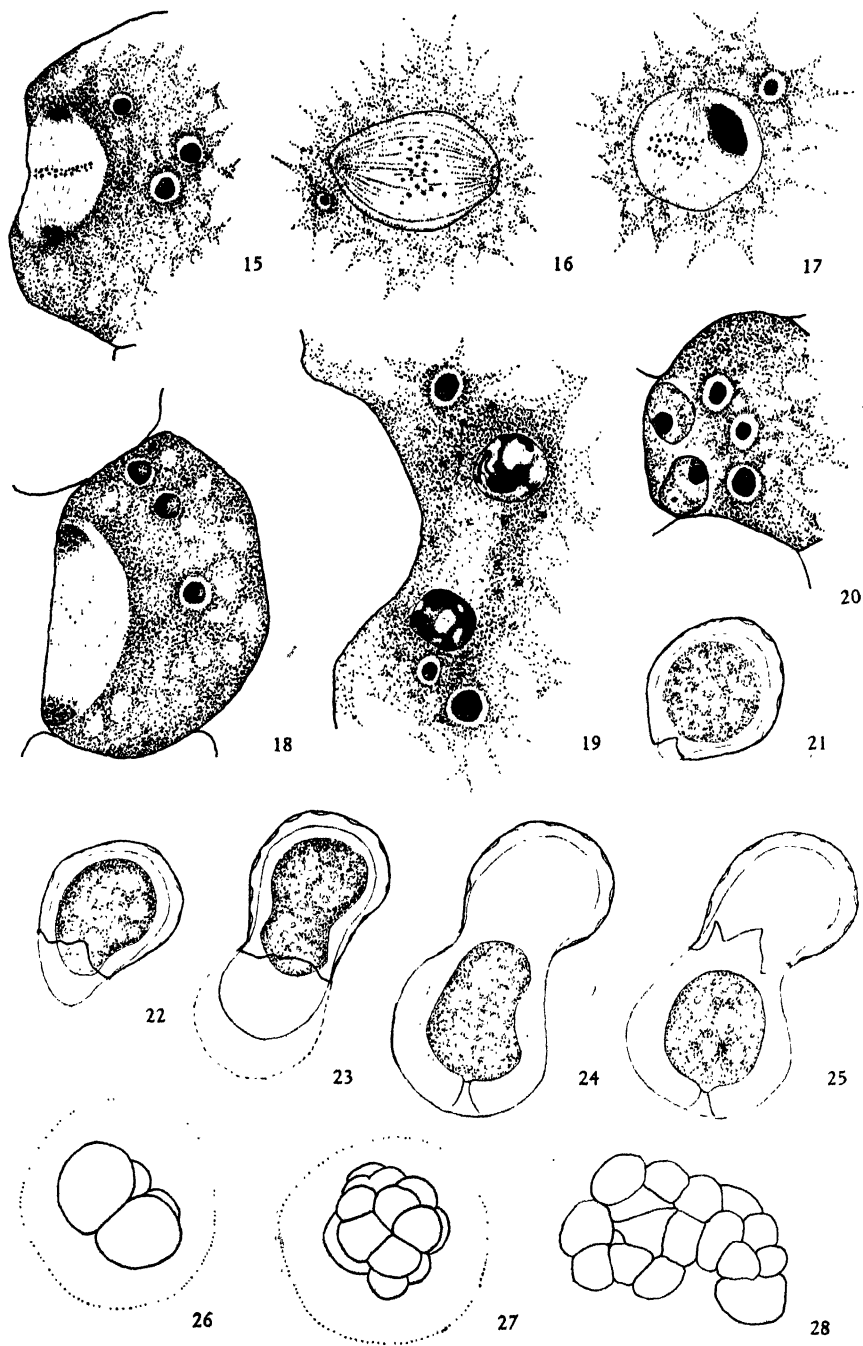
sion. (2) Female sex cells, each forming one oogonium and egg. (3) Male sex cells, each dividing to form a sperm platelet of 128 biflagellated sperms. All reproductive cells are biflagellated in their early stages of development. The flagella are lost as development and differentiation proceed.

**Reproductive Cycle.** Mother colonies may contain asexual, male, or female offspring, or combinations of these, except that the occurrence of males and females within the same mother has not been observed in *V. Carteri*. There seems to be a definite sequence in the types of daughters produced in a population. At the beginning of a cycle asexual daughters predominate for some time. Later males begin to appear and increase in number, while female colonies begin to occur still later. Asexual colonies are produced throughout the cycle, but the proportion of these varies, tending to diminish as the sexual stages flourish. At the height of the sexual phase of the cycle males and females occur in almost equal proportions. Shortly after, the proportion of males falls off rapidly while that of females remains high. Toward the end of the cycle the proportion of females may exceed that of asexual colonies (fig. 46), whereas practically no males can be found. The females then begin to disintegrate, settle down to the substratum and release their oospores as they break up. Only asexual colonies remain, and these initiate a new cycle. If environmental conditions are suitable, after a brief period of rest the oospores germinate. During the sexual phase, *Volvox* colonies are continually produced asexually. When environmental conditions become unsuitable, asexual production of colonies ceases almost abruptly, and the oospore undergoes a prolonged resting period until suitable environmental conditions are restored. Then germination of oospores occurs almost simultaneously, resulting in the production of large numbers of juvenile colonies (to be described later), and these give rise to the usual type of *Volvox* colony.

#### Explanation of figures 1-14

All of the drawings were made with the aid of a camera lucida using a Bausch and Lomb microscope with 10 $\times$ , 43 $\times$ , and 97 $\times$  objectives in combination with various oculars. The photographs were taken with a Leica camera Model F. FIG. 4  $\times$  970, others  $\times$  1200.

FIGS. 1-5. Nuclear division during interphase, endosomes in various stages of vacuolization. Note the nucleus with large vacuolated endosome and small plasmosome in figure 1. In figure 3 the nucleus contains two small chromatic bodies (plasmosomes?) in addition to the endosome. FIG. 6. Nucleus during prophase; polar masses are connected by granular threads. FIG. 7. Nucleus during prophase showing chromatic substance left behind after endosomal division. FIG. 8. Nucleus during prophase with lobed polar masses, chromatic granules persistent between them. FIG. 9. Nucleus during prophase showing early stages of extrusion of polar masses, the intranuclear portions with long fingerlike processes. FIG. 10. Nucleus during prophase with polar masses unlobed, ellipsoidal, vacuolated and partially extruded through the nuclear membrane. FIGS. 11-13. Nuclei during prophase with intranuclear portions of the polar masses deeply stained. FIG. 14. Nucleus during prophase with numerous chromatic bodies consisting of bivalent chromosomes, endosomal granules, and at the left an intranuclear portion of a polar mass.



**Asexual Reproduction.** Gonidia are differentiated at about the 64-celled stage of development of a daughter colony. All the reproductive cells ultimately reach a large size through growth. Once the gonidia are differentiated, they do not undergo subsequent division before the young colony is liberated from the parent. As they increase in size, the reproductive cells protrude into the interior of the colony until they occupy a position just below the peripheral row of vegetative cells, leaving behind a clear area, filled with gelatin, denoting their former position.

Gonidia are characteristically eight in number in a colony, occurring in two tetrad groups arranged in two parallel planes within the coenobium; one is just anterior to the equator and the other about half-way between the equator and the posterior pole (fig. 43). The members of one tetrad group alternate with the members of the other group. The precise mathematical arrangement of the tetrad groups has been stressed by Powers (1908) and Shaw (1922b). Gonidia remain biflagellated until after inversion of the developing colony. Inverting colonies, crushed under the cover glass, sometimes have a few of their gonidia torn free into the surrounding fluid and each possesses two flagella waving from a slightly depressed portion of the margin. The exact time of loss of these flagella could not be determined, but gonidia of everted and well developed daughter colonies no longer possess them. Usually, gonidia do not divide until after the extrusion of the daughter colony. Before division they attain about 80  $\mu$  in diameter. A mature gonidium is sharply characterized not only by its large size, but also by its highly vacuolated contents, prominent nucleus and numerous pyrenoids (figs. 49, 50). Vacuolization extends even to the chloroplast.

A detailed description of the stages of development of the gonidium of *V. aureus* prior to inversion has been given by Janet (1923b), and Pocock (1933b) has written a complete account of the inversion process in *V. Rous-*

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#### Explanation of figures 15-28

FIGS. 15-19  $\times 1200$ . FIG. 15. Nucleus at early anaphase, traces of the polar masses persistent, chromosomes markedly condensed. FIG. 16. Nucleus during anaphase, polar masses no longer visible. (Not all the chromosomes are shown in this figure.) FIG. 17. Nucleus during anaphase, showing an undivided endosome lying outside of the spindle. FIGS. 18, 19. Telophases. FIG. 20. Interphasic daughter nuclei, endosomes and plasmosomes present.  $\times 970$ . FIGS. 21-28. Germination of the oospore and development of the juvenile colony.  $\times 430$ . FIG. 21. 9 Je 41. Oospore, mesospore protruding from ruptured exospore. 9: 30 a.m. FIG. 22. 9 Je 41. The same oospore at 10: 20 a.m. FIG. 23. 9 Je 41. The same oospore at 10: 35 a.m. FIG. 24. 9 Je 41. The same oospore at 11: 05 a.m.; the mesospore and protoplast have been almost completely extruded from the exospore. The delicate endospore is visible. Two flagella project from a colorless beak at the anterior end of the zoospore. FIG. 25. 9 Je 41. The same oospore at 11: 20 a.m. FIG. 26. 9 Je 41. 4: 30 p.m. The zoospore has lost its flagella and has undergone two divisions. FIG. 27. 9 Je 41. 7: 00 p.m. Further divisions have resulted in the formation of an irregular mass of cells. FIG. 28. Cell masses of developing juvenile colonies flattened by coverslip pressure.

*seletii* and *V. capensis*. Because division of the gonidium and development of the daughter colony of *V. Carteri* follow the general pattern described by these authors, only a brief description of the process will be presented in this study, with emphasis accorded to features peculiar to *V. Carteri*.

Gonidia begin to divide shortly after the release of daughter colonies from the parent coenobium. The plane of the first division is anticlinal (fig. 51). Both daughter cells are strongly incurved at the center of the plane of division, so that a hollow is formed between them (fig. 57). In the second division the plane is also anticlinal but frequently oblique to the first plane of division (figs. 52, 53).

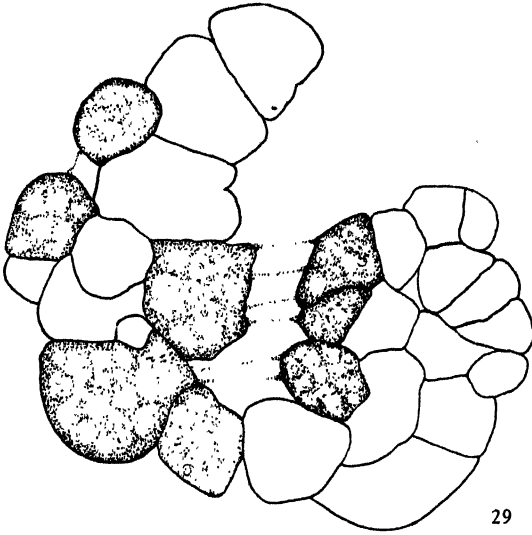
The anterior physiological polar axes of the cells become progressively inclined toward one another as division proceeds (Zimmerman 1923) so that a characteristic bowl-shaped configuration is formed after the third division. This shape is maintained thereafter by anticlinal divisions. At the eight-celled stage of development (figs. 34, 35, 54) four of the cells slip below the remaining four. A shift in the physiological polar axes of these cells is brought about by reorientation of their contents, so that their axes become radii of the developing daughter. Figure 58 shows the 16-celled stage flattened by the cover glass. There are strong indications that the four large triangular peripheral cells divide later to form the eight gonidia of the next generation. This cannot be stated with certainty because it is difficult to trace individual cells beyond the 16-celled stage. Differentiation of the gonidial initials probably occurs at the 32- or 64-celled stage. In figure 36, approximately the 64-celled stage, the eight gonidia are clearly differentiated. Cells of the developing daughter colony divide synchronously with the exception of the differentiated reproductive cells. Cytological preparations show all the vegetative cells of a developing daughter colony in almost exactly the same stage of mitosis (fig. 100).

Cells of the developing colony have chloroplasts containing one or more pyrenoids. The colony is in contact with the external medium by means of the portion of the vesicle located on the surface of the mother colony. As division proceeds, the cells become progressively smaller and more compactly arranged. At this stage the phialopore is small and rests just below the

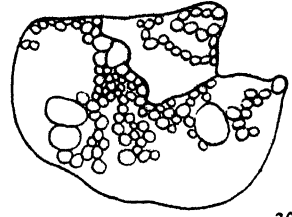
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#### Explanation of figures 29-36

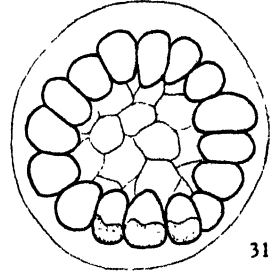
FIG. 29. Flattened juvenile colony showing protoplasmic connections between cells.  $\times 860$ . FIG. 30. Bowl shaped juvenile colony formed fifteen to twenty minutes after the stage figured in 29. About four large reproductive cells bulge from the outside of the bowl which later everts.  $\times 430$ . FIG. 31. Cup shaped developing sperm platelet before eversion.  $\times 970$ . FIG. 32. Spermatozoid.  $\times 970$ . FIG. 33. Curved sperm platelet.  $\times 540$ . FIG. 34. 8-celled cruciate stage in the development of a daughter colony. FIGS. 34-36  $\times 970$ . FIG. 35. 8-celled stage in the development of a daughter colony. Four corner cells have slipped below the remaining four. FIG. 36. Approximately the 64 celled stage of development of a daughter colony. The eight reproductive cells of the next generation are already differentiated.



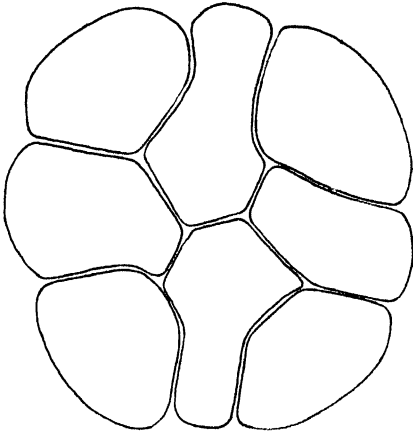
29



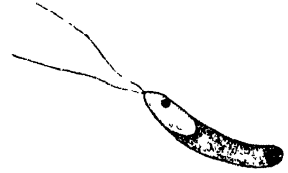
30



31



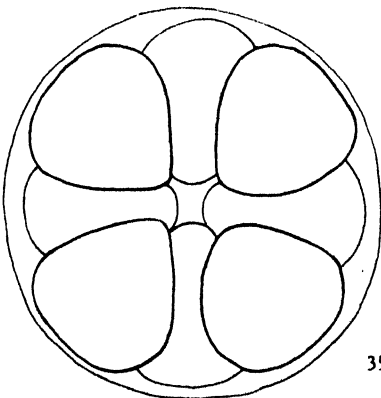
34



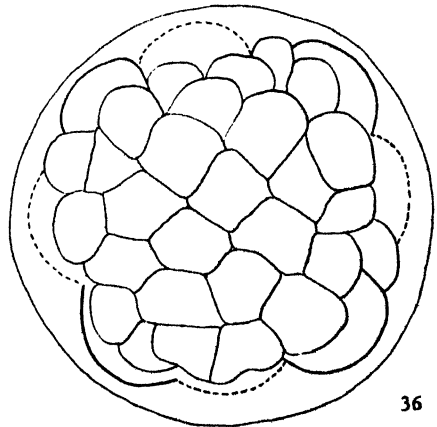
32



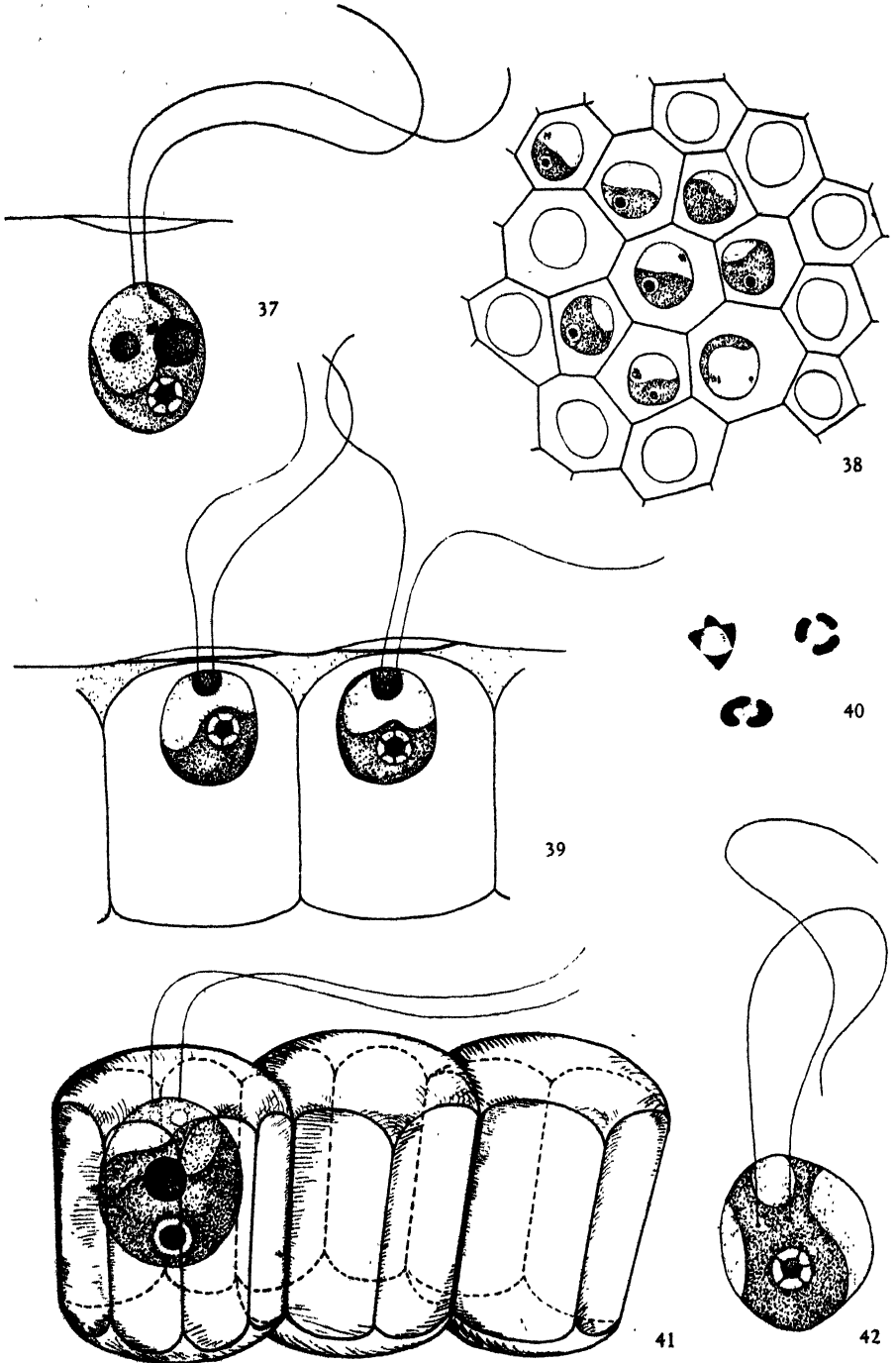
33



35



36



surface of the mother colony. Soon it becomes larger and irregular. In figure 63 the gonidia project outwardly from the surface and an enlarged phialopore is evident.

Inversion begins with a folding of the lobes (usually four) of the phialopore (fig. 59) into the hollow center of a daughter colony. At about the same time, the portion of the daughter directly opposite the phialopore begins to invaginate and continues to do so while the infolded lobes begin to straighten out. Pocock (1933) points out that changes in the shape of the cells, the appearance of flagella and protoplasmic connections at this time are essential factors in the inversion process in the forms she observed. The lobes of the phialopore become reflexed outward (fig. 60) over the exterior of the colony and proceed to fold over the colony until inversion is completed (figs. 61, 62, 64). Pocock (1938) was able to see protoplasmic connections in the cells of the phialopore lobes, and in some cells of the completely inverted daughters of *V. tertius* and *V. gigas*. In *V. Carteri* protoplasmic connections in recently everted daughters were seen on few occasions, but, as will be shown later, protoplasmic strands are clearly evident connecting the cells of developing juvenile colonies. After eversion, the lobes of the phialopore come together, fold over the pore and completely close it so that it can no longer be detected. An optical section (fig. 65) through the colony at this stage shows the well developed gonidia inside the colony. In surface view (fig. 66) the protoplasts are polygonal because of mutual compression and because the prism walls have not developed to any noticeable extent. At this stage stigmata appear, the flagella lengthen, the daughters increase in size and begin to move very slowly within their vesicles. Movement increases until rotation is distinct. Figure 47 shows two young colonies forced out of the mother by cover glass pressure and still enclosed by their vesicles. When fully mature, each colony escapes through the ruptured wall of the mother coenobium. Sometimes the mother colony breaks up after one or two daughter colonies have been discharged, thus releasing the remainder. Soon after birth, the gelatinous prism walls swell, separating the protoplasts which then lose their angular shape and become round in surface view.

Inversion occurs almost immediately after cell division is completed. Daughters in various stages of development and inversion were to be seen

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#### Explanation of figures 37-42

FIG. 37. Protoplast of a vegetative cell. Note the common colony membrane.  $\times 1455$ . FIG. 38. Group of 17 vegetative cells in surface view stained with methylene blue to reveal membrane structures. There are 4 pentagonal, 9 hexagonal and 4 heptagonal shaped cells visible.  $\times 970$ . FIG. 39. Living vegetative cells in longitudinal optical section showing membrane structure.  $\times 970$ . FIG. 40. Pyrenoids showing spherical centers with 2, 3 and 4 starch plates arranged around them.  $\times 1200$ . FIG. 41. Schematic diagram of three adjacent *Volvox* prisms, 5, 6 and 7 sided to show the cell and membrane structure; colony envelope not shown.  $\times 1900$  approx. FIG. 42. Protoplast of an anterior vegetative cell.  $\times 1940$ .



in samples of living *Volvox* taken at almost any time of the day or night. Later, in the cytological portion of this paper, it will be shown that there is evidence for two periods of maximum mitotic activity; one occurring in the afternoon at about 3 o'clock and the other in the evening at about 10 o'clock. Periods of maximum occurrence of inversion are directly correlated with these times of maximum cell division.

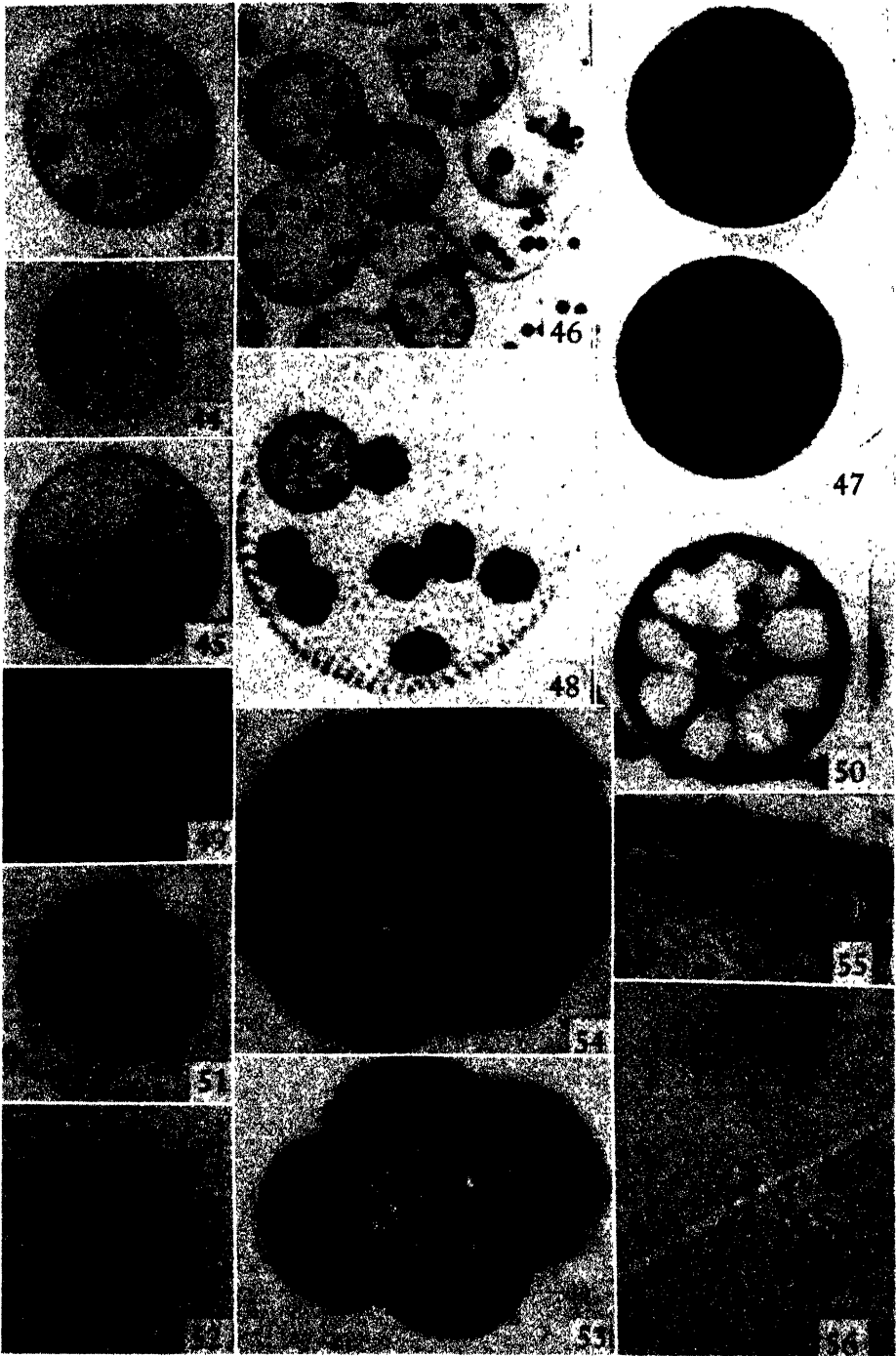
**Sexual Reproduction.** Just before birth, male colonies (fig. 44) are larger than either female or asexual colonies. After birth, however, there is little increase in size, whereas the other two types of colonies become considerably larger. The ultimate differences in size are due to the number of cells in each type of colony. Females have somewhat fewer cells than asexual colonies, but the males have from one-eighth to one-third the number of either of these.

Males are easily distinguished from the other two types of colonies by the relatively large number (50) of reproductive cells scattered all over each colony with the exception of a small area near the anterior pole (fig. 44). Asexual colonies have eight reproductive cells arranged in tetrads and female colonies have about 20 oogonia occupying the posterior two-thirds of the coenobium. Of all the types of reproductive cells, antheridial initials are the smallest and least differentiated from the vegetative cells. They lack the vacuolization of the gonidia and the dense protoplasm filled with storage material found in oogonia. Division generally begins just before the birth of the male colony and continues thereafter. Before division, a large number of pyrenoids have developed inside each antheridial initial. These become divided among the products of antheridial initial division until finally each spermatozoid possesses a single pyrenoid. Usually each

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#### Explanation of figures 43-56

FIGS. 43-45  $\times 280$ . FIG. 43. Young asexual colony with 8 daughter colony initials. FIG. 44. Male colonies bearing numerous (about 50) sperm plate initials. FIG. 45. Mature female colony containing 16 oogonia. FIG. 46. Group of female colonies showing their predominance at the end of the sexual phase in the life cycle.  $\times 130$ . FIG. 47. Young asexual colonies forced out of the mother colony by cover glass pressure, with their outer gelatinous membranes still intact.  $\times 1000$ . FIG. 48. Asexual colony showing lack of synchronous development of daughter colonies. Of 8 developing daughters one is almost completely developed, while the others are in very early developmental stages.  $\times 450$ . FIG. 49. Living daughter colony initial (gonidium).  $\times 1000$ . FIG. 50. Sectioned and stained gonidium. Note the vacuolated protoplast in which several pyrenoids are scattered and the nucleus containing an endosome and plasmosome.  $\times 2500$ . FIG. 51. First division of the gonidium; from living material.  $\times 1000$ . FIG. 52. 4-celled stage of a developing daughter colony; from living material.  $\times 1000$ . FIG. 53. 4-celled stage of a developing daughter colony; from living material.  $\times 2400$ . FIG. 54. 8-celled stage of a developing daughter colony.  $\times 2400$ . FIG. 55. Cytological preparation of a section through a group of vegetative cells of an adult colony.  $\times 2500$ . FIG. 56. Vegetative cell, living condition. Note the pyrenoid at the posterior end, two contractile vacuoles at the anterior end, and flagella.  $\times 5600$ .



antheridial initial undergoes seven divisions resulting in a cup-shaped mass of cells (figs. 31, 67, 68, 69). Flagella appear during the inversion which immediately follows cessation of division. Sperm platelets are convex on their flagellated surfaces and concave posteriorly (figs. 33, 70). Shortly after inversion, the eyespots are formed. Spermatozooids appear like elongated vegetative cells (fig. 32). Each has a cup-shaped chloroplast, pale green in color, with a single pyrenoid located at the posterior end; two contractile vacuoles occur in the clear, pointed apical portion of the cell near the stigma and two flagella, approximately the same length as the body of the spermatozoid, project from the anterior tip.

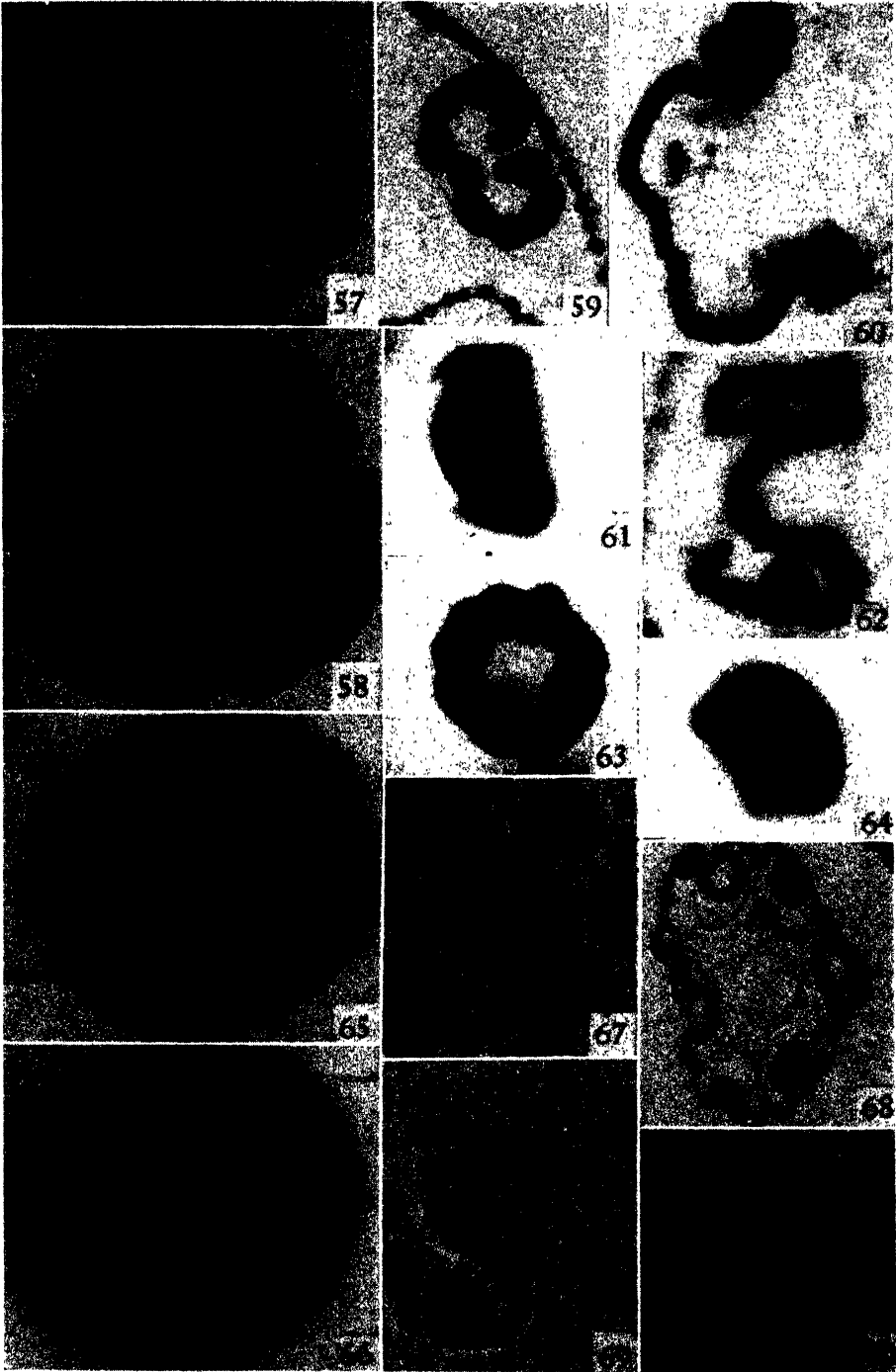
When sperm platelets are mature, they begin to rotate within their vesicles as their flagella slowly beat. Flagellar movement increases until each platelet emerges through a pore in the external gelatin of the parent originally formed by the descending antheridial initial cell. All platelets are not released at the same time but over a period of time, during which the male colony is in vigorous motion. A short time after all the platelets have been released, the male colony usually breaks up. Once the platelet is free from the parent it moves rapidly through the water. The association of spermatozooids in a platelet is maintained for a prolonged period.

Female colonies (fig. 45) are only slightly smaller than asexual colonies and are distinguished from the latter by the larger number (usually 18 to 20) and specialized character of reproductive cells. As oogonia become differentiated in size from vegetative cells, they become greener, and their

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#### Explanation of figures 57-70

FIG. 57. Cytological preparation of a section through the 2-celled developing daughter colony. Note the endosome and plasmosome in the nucleus of the cell on the left.  $\times 2150$ . FIG. 58. 16-celled developing daughter colony flattened by cover glass pressure. Note 4 larger cells which will become reproductive cells.  $\times 2400$ . FIG. 59. Median section through a developing daughter colony; beginning of eversion; phialopore lips and opposite pole invaginating.  $\times 1000$ . FIG. 60. Median section through a daughter colony, color older than preceding. The phialopore lips now fold outward. Note the reproductive cell projecting from the outside of the colony (upper portion of figure).  $\times 2100$ . FIG. 61. Lateral aspect of developing daughter colony; phialopore lips folding downward moving past the remainder of the colony (living material).  $\times 1000$ . FIG. 62. Cytological longitudinal section of approximately the same stage of eversion as shown in figure 61. Note the large reproductive cells within the backfolding lips.  $\times 2100$ . FIG. 63. Phialopore view of a living daughter colony before eversion. The large reproductive cells project from the outside surface.  $\times 1000$ . FIG. 64. Lateral view, living daughter colony. Eversion process almost completed, the reproductive cells visible within the colony.  $\times 1000$ . FIG. 65. Optical section through a living daughter colony after eversion.  $\times 2900$ . FIG. 66. Surface view of a living daughter colony after eversion. The protoplasts are angular due to mutual compression.  $\times 2900$ . FIGS. 67-70. Stages in the formation of a sperm platelet. FIG. 67. First and second divisions of sperm initial cells.  $\times 1700$ . FIG. 68. Stained section through a male colony showing an initial cell and various stages in the development of sperm platelets.  $\times 1000$ . FIG. 69. Immature sperm platelet after eversion in surface view, containing 128 cells.  $\times 3800$ . FIG. 70. Lateral view of a mature sperm platelet; note eyespots and flagella.  $\times 3800$ .



protoplasts become densely packed with storage material. In *V. tertius*, a species bearing strong resemblance to *V. Carteri*, the oogonia and gonidia have almost the identical vacuolated appearance. Oogonia of *V. Carteri* are sparsely vacuolated. In the living condition their dark green, opaque appearance is striking. Of the three types of reproductive cells produced by *Volvox*, the oogonium is the only one which does not undergo subsequent division. Janet (1922) found in *V. globator* a "blastéa oosphérique" of 64 cells consisting of one large oosphere surrounded by an ephemeral syncytial follicle of 63 abortive oospheres which soon become resorbed without leaving a trace. There is no evidence that division of the female reproductive cell occurs in *V. Carteri*.

Mature eggs of *V. Carteri* (figs. 71, 72) are almost spherical, about 48  $\mu$  in diameter, and contain a great number of pyrenoids (larger than those of the vegetative cells), fatty globules, and material which responds positively to the chemical tests for volutin.

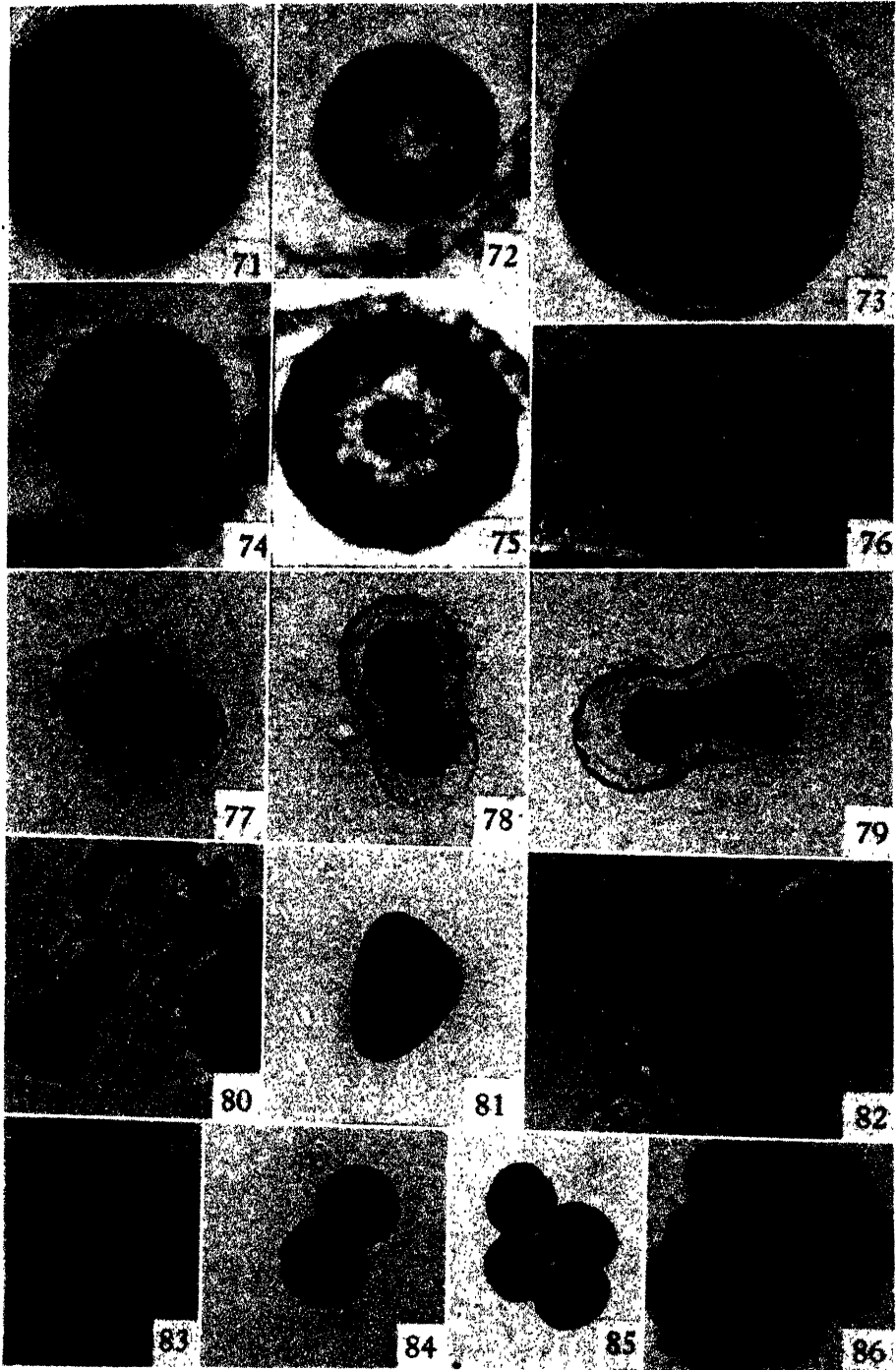
Although observations were made on many hundreds of female colonies containing oogonia in all stages of development, on no occasion were sperms found within the female colony or near the oogonia. In observations made on *V. perglobator* sperms were easily detected in close contact with the outer wall of almost any oogonium. Many of the sperms persisted on the outside long after the oospore wall had become differentiated. Microtome sections of *V. perglobator* show sperms on the periphery of oogonia and oospores. Overton (1889) and Lander (1929) have described male nuclei within the oosphere in *V. aureus* and *V. globator*, but Pocock (1933) believes that they may have been binucleate oospheres such as she observed in *V. Rousseletii*.

The fact remains that fertilization has not been authentically observed in any species of *Volvox*, although Zimmerman's (1921) description of zygotic meiosis in *V. aureus* indicates that it does occur. On the other hand, Mainx (1929a) showed that parthenogenetic development of eggs occurs commonly in *V. aureus*. Thus it would appear that eggs of *Volvox* may develop either parthenogenetically or after fertilization. It is possible that eggs may develop parthenogenetically in *V. Carteri*, but this cannot be stated with certainty.

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#### Explanation of figures 71-86

FIG. 71. Optical section of a living oogonium containing storage material and pyrenoids.  $\times 3000$ . FIGS. 72-75  $\times 2500$ . FIG. 72. Stained median section of an oogonium. FIG. 73. Living oospore in optical section. FIG. 74. Stained section through an oogonium showing a small nucleolus adjacent to the oogonium endosome. FIG. 75. Stained section through an oospore. FIGS. 76-82. Germination of the oospore. (Living material.) Note the cleft exospore, thick mesospore and delicate endospore in figure 80.  $\times 1000$ . FIG. 83. Aplanospore surrounded by mesospore, endospore not visible.  $\times 1000$ . FIGS. 84, 85. First and second divisions of aplanospore.  $\times 1000$ . FIG. 86. Irregular mass of cells formed after further divisions. At the right one large reproductive cell is visible.  $\times 2000$ .



Whatever their origin, the oospores become increasingly darker green and denser as they mature. Three walls or membranes are secreted by the developing oospore (figs. 73, 75): a delicate endospore closely attached to the protoplast, a rather thick mucilaginous mesospore, and finally, a tough exospore with a reticulately ridged surface. At first these membranes are indistinguishable, but after the oospore has matured, its protoplast contracts a little, showing the exospore and mesospore clearly. The endospore is usually so closely adherent to the protoplast as to be indistinguishable in the resting oospore, but it is frequently clearly evident during germination stages (figs. 24, 80). After the walls have been laid down, the oospore begins to change its color from dark green to an orange-brown. A fully ripened oospore has an exospore slightly wavy in outline because of surface reticulation, an underlying mucilaginous mesospore, and a centrally located orange-brown protoplast bounded by a close-fitting, delicate endospore. The orange-brown color of the oospore has been ascribed to the presence of an orange-red oil (Klein 1889a), carotin (Overton 1889; Zimmerman 1921), and to haematochrome (Pocock 1933b). When moribund females finally break up, their oospores are released and come to rest on the bottom. They germinate a short time later (see germination chart below) if conditions are favorable.

Cienkowski (1870) observed the production of aplanospores from germinating oospores of *V. aureus*. Zimmerman (1921) mentions that the external progress of germination of oospores of *V. aureus* is the same as described by Kirchner (1879), and reports that meiotic division occurs, resulting in the formation of a haploid aplanospore. Mainx (1929a) found that oospores were developed parthenogenetically in *V. aureus* under certain conditions, and that these parthenospores germinated in exactly the same fashion as described by Kirchner (1879) and Henneguy (1879). In oospore cultures of *V. Rousseletii* (Pocock 1933c) and of *V. tertius* (Pocock 1938) the first record of biflagellate *Chlamydomonas*-like zoospores was obtained by Pocock, who suggested (1938) the possibility that aplanospores are formed from parthenospores and zoospores from zygotes.

In attempting to obtain germination, moribund females were drawn up with a pipette from the bottom of a jar containing *Volvox* and placed into small petri dishes. Sometimes healthy females were removed from a mass collection and allowed to reach maturity in dishes containing one of the culture media employed in these experiments. In either case, after the female colonies disintegrated, the oospores were shed. Three types of fluid were used for germination experiments: (1) filtered water from the source in which *Volvox* was found; (2) Moewus' cold soil extract diluted as follows: one part extract, ten parts glass distilled water (Moewus 1940); (3) synthetic medium (Uspenski and Uspenskaja 1925). Spores from a given *Volvox* collection were separated into these three media at one time.

Germination occurred in solutions 2 and 3, but no germination occurred in solution 1 nor in certain combinations of the three solutions.

An effort was made to germinate dry spores, Pocock (1933b) having found with spores of *V. Rousseletii* and *V. capensis* that "completely drying was not essential but beneficial." In this study only wet spores were viable. A small percentage of germination occurred in Moewus' fluid, but about 90 per cent germination was obtained with Uspenski's fluid.

TABLE 1. *Data on Germination of Oospores.*

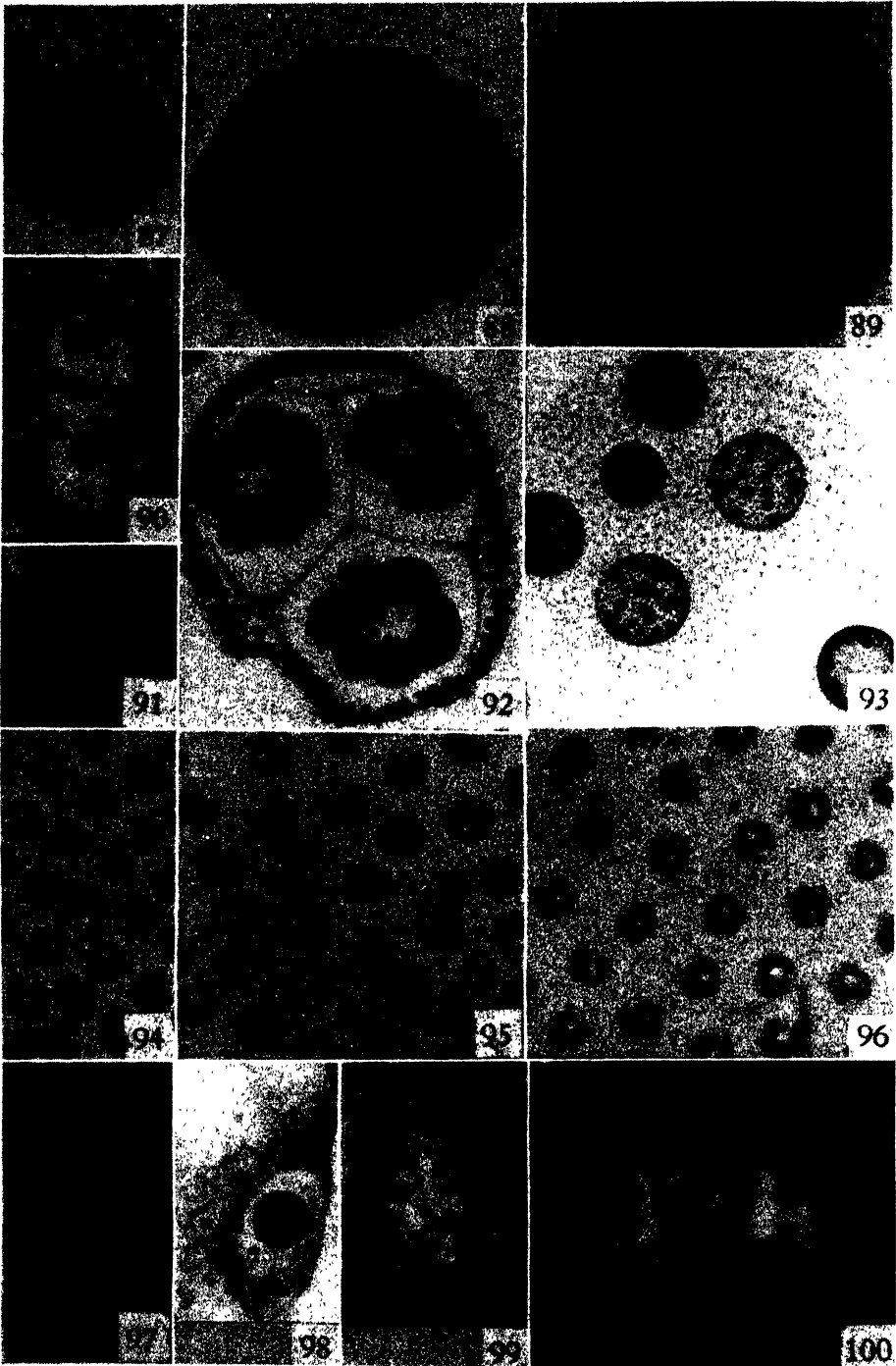
A	B	C	D
Date of collection of material	Date oospores placed in culture fluid	Culture fluid	State of oospores
27 My 41	7 Je 41	Moewus 10%	Wet
27 My 41	17 Jl 41	Moewus 10%	Wet
18 Jl 41	22 Jl 41	Moewus 10%	Wet
18 Jl 41	24 Jl 41	Moewus 10%	Wet
		Uspenski	Wet
18 Jl 41	25 Jl 41	Moewus 10%	Dry
		Uspenski	Dry
18 Jl 41	31 Jl 41	Moewus (10%) + Uspenski (20%)	Dry
		Moewus 10%	Wet
18 Jl 41	8 Jl 42	Tricker's water	Wet
6 Au 42	16 Au 42	Tricker's water	Dry
		Uspenski	Wet

E	F	G
Date of germination	Duration of rest period of oospores (days)	Time required for germination (days)
9, 10 Je 41	12	3-4
18, 19, 20, 21 Jl 41	52	1-5
23 Jl 41	5	1-2
28 Jl 41	7	5
29 Jl 41	7	6
No germination	8	
" "	8	
" "	8	
4 Au 41	14	5
No germination	14	
No germination	1 year	
17 Au 42	11	1-2

With the aid of a binocular dissecting microscope, oospores in a minimum amount of fluid were drawn up into a thin pipette and transferred to a dish containing sterile culture fluid. Care was taken to exclude detritus and visible microorganisms. Spores were washed by several transfers into dishes containing fresh culture fluid. By this procedure contamination of the culture fluids was reduced to a minimum.

Petri dishes (1½-2½ inches in diameter) containing oospores and culture fluid were placed on glass shelves in a glass cabinet situated in front of a





window facing approximately north. Light from three 100-watt daylight bulbs, one on each side and one above, supplemented the daylight illumination during the day as well as at night.

All the stages of germination shown in the photographs (figs. 76-89) were derived from spores in Uspenski's fluid. The camera lucida drawings (figs. 22-30) illustrate germination stages of spores placed in Moewus' solution. The latter produced biflagellate zoospores and those in Uspenski's fluid yielded aplanospores. Either germination product, aplanospore or zoospore, gave rise, after successive divisions followed by inversion, to juvenile colonies (figs. 87-89). Obviously the conditions under which oospores were germinated in the laboratory differ somewhat from the conditions which obtain in nature. These experiments were not planned to determine the factors that control germination of the oospores, but rather were intended to induce germination so that successive stages could be observed and described.

An oospore about to germinate is easily recognized by its characteristic vesicular appearance (figs. 21, 76) apparently caused by the swelling of the mesospore which forces the protoplast to contract and become more dense.

A summary of the stages in the germination of an oospore follows: As stated above, oospores in Moewus' solution produce biflagellate zoospores, while those in Uspenski's fluid give rise to aplanospores. The history of the formation of aplanospores and zoospores is more or less the same, but for the development of a flagellar apparatus in the latter. Evidently, the swelling of the mesospore proceeds to such an extent that the exospore is

#### Explanation of figures 87-100

FIG. 87. Everted juvenile colony containing large reproductive cells.  $\times 1400$ . FIG. 88. Optical section through juvenile colony.  $\times 2400$ . FIG. 89. Surface view of a juvenile colony showing polygonal protoplasts containing numerous oil globules derived from the oospore.  $\times 2400$ . FIG. 90. Two nuclei showing endosomes with buds attached; the endosome stains heavily and the bud less so.  $\times 4800$ . FIG. 91. Anaphase of mitosis. This is the preparation from which figure 17 was prepared. Note the endosome lying outside of the spindle.  $\times 4800$ . FIG. 92. Section through an asexual colony stained with methylene blue, showing the membrane structure. Note the thick prism membranes of the daughter colonies meeting near the center of the colony, and the colony membrane surrounding each daughter colony.  $\times 1400$ . FIG. 93. Crushed mother colony containing four asexual daughter colonies and two male colonies.  $\times 250$ . FIGS. 94-96  $\times 4800$ . FIG. 94. Protoplasts from posterior pole of a colony showing close proximity and lack of eyespots. FIG. 95. Protoplasts from the equatorial region of a colony; protoplasts more separated, some with small eyespots. FIG. 96. Protoplasts from the anterior pole of a colony; widely separated and all with large eyespots. FIG. 97. Surface view of a portion of a colony treated with methylene blue to show the membrane structure.  $\times 2100$ . FIG. 98. Interphasic nucleus of a gonidium containing a large vacuolated endosome and a small plasmosome.  $\times 4800$ . FIG. 99. Prophasic nucleus containing a divided endosome, the polar masses connected by granular threads.  $\times 7500$ . FIG. 100. Nuclei at metaphase, illustrating synchrony of nuclear division in developing daughter colonies.

finally cracked by internal pressure; but other factors may be involved in the rupture. The mesospore projects through the cracked exospore (figs. 22, 76, 77) and continues to swell, thus widening the aperture (figs. 23, 78, 79, 80, 82) to permit finally the emergence of the entire mesospore together with its enclosed protoplast, leaving the empty exospore behind (figs. 24, 25, 80). When the contents of the spore have emerged about half-way (figs. 24, 25), a small clear beak or papilla develops at the anterior end of the protoplast and here soon afterward two short flagella are formed. These protrude through the endospore and wave feebly in the watery gelatinous substance of the mesospore. At this stage the endospore is clearly defined as a delicate membrane adhering closely to the anterior and posterior ends of the emerging protoplast but separated laterally (fig. 24). The greater part of the protoplast is extruded in about one hour; the remainder is discharged very rapidly. The liberated zoospore is distinctly *Chlamydomonas*-like, somewhat ellipsoidal, reddish-brown in color, with numerous oil globules and an anterior colorless beak from which two flagella project (fig. 25). While the zoospore moves slowly around by means of its flagella, it becomes somewhat enlarged and develops small green areas in the chloroplast. Finally, the flagella are lost and division begins.

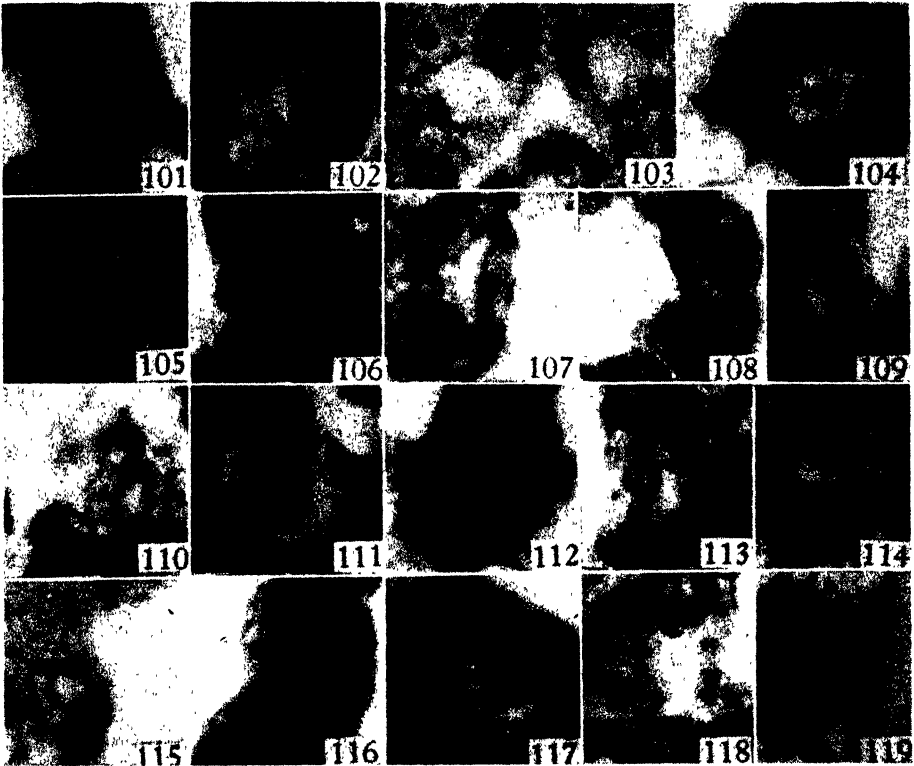
Liberated aplanospores are usually asymmetrical (fig. 81) but eventually become spherical (fig. 83), and then proceed to divide (figs. 84, 85). There is no sign of a flagellar apparatus nor is a beak formed.

The entire content of the oospore is given over to the formation of a single product, aplanospore or zoospore. On no occasion was there evidence of the formation of vestigial cells such as occur in the germination of oospores of *Eudorina* (Schreiber 1925) and which are believed to be suggestive of meiosis.

Each germinating oospore of *Volvox* generally contains a single nucleus which becomes incorporated into the germination products, aplanospore or zoospore. Infrequently, microtomed sections of germinating oospores reveal from two to four nuclei. Although about 100 germinating oospores were fixed at various stages and later sectioned and stained, there was no evidence of any meiotic activity except in the instances just mentioned.

From this point on, both oospore products have practically the same development. As division proceeds, the mesospore gradually becomes more and more hydrolyzed and finally disappears completely. After a few divisions (figs. 26-28), an irregular mass of cells, some of which are connected by distinct protoplasmic strands, is produced (fig. 29). Some distinctly larger cells (three or four) may be seen (fig. 86). These are the reproductive cells of the developing juvenile colony. Later the mass becomes oriented forming an irregular bowl with four indistinct lobes and three or four well differentiated, large reproductive cells, projected exteriorly (fig. 30). Inver-

sion then occurs and a motile juvenile colony is produced (fig. 87). This is scarcely larger than the original zoospore or aplanospore, since division proceeds rapidly with little, if any, growth. The colony is still rather brownish in appearance at this stage. A surface view reveals polygonal protoplasts



FIGS. 101-116. Intranuclear mitosis in vegetative cells of *V. Carteri* var. *Hazeni* involving endosomal division and extrusion. FIGS. 108 and 114  $\times 2400$ , others  $\times 4800$ . FIG. 101. Interphase. FIGS. 102, 103. Division of the endosome. FIG. 104. Partial extrusion of a polar mass through the nuclear membrane. FIG. 105. Polar mass at top of nucleus and chromatic masses scattered throughout. FIG. 106. Chemical change occurring in a polar mass. The fingerlike portions within the nucleus stain deeply with nuclear dyes; the outer portions stain lightly or not at all. FIGS. 107-109. Metaphases-early anaphases with slight traces of polar masses visible. FIGS. 110-112. Anaphases; no trace of polar masses visible. FIGS. 113-115. Telophases. FIG. 116. Karyokinesis completed, cytokinesis beginning. FIG. 117. Division of a pyrenoid.  $\times 4800$ . FIG. 118. Nuclear reorganization after nuclear division.  $\times 2400$ . FIG. 119. Formation of massive endosomes in daughter nuclei.  $\times 4800$ .

closely crowded together and containing numerous translucent oil globules (fig. 89). Their brownish color, small size, and oil globules sharply characterize young germ colonies. In optical section about four or five large reproductive cells, projecting into the interior, are visible (fig. 88).

Protoplasmic strands connect the cells throughout the development of a juvenile colony, even during inversion. Finally, prism walls are developed around the protoplasts, which gradually become rounded and greenish. During this process all protoplasmic connections disappear. The resultant juvenile colony is smaller and has fewer gonidia and vegetative cells than the vegetative *Volvox* colonies and differs in color. One or two, generally not all the gonidia in the juvenile colony undergo division and inversion and form asexual *Volvox* colonies. Pocock (1933) found that the daughters of juveniles were transitional between juveniles and the normal adults formed in succeeding generations.

### LIFE CYCLE OF VOLVOX CARTERI

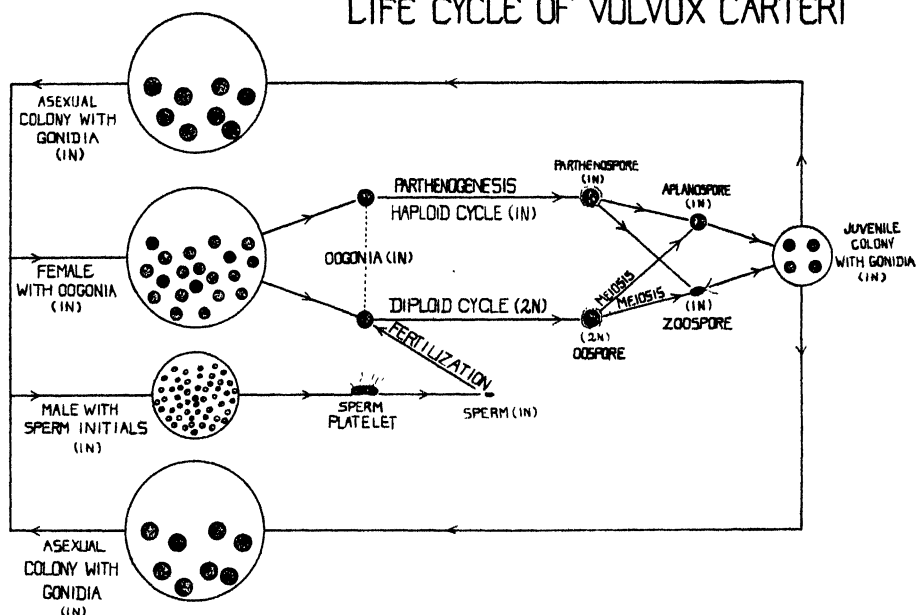


FIG. 120. The life cycle of *Volvox Carteri*.

In this study the formation of either aplanospores or zoospores was observed under different cultural conditions. Aplanospores were formed in synthetic medium (Uspenski & Uspenskaja 1925) and zoospores in soil extract (Moewus 1940). Other factors probably influence the development of the flagellar apparatus, but, undoubtedly, the medium in which the spores are germinated plays an important role. Pocock's conjecture (1933b) that parthenospores form aplanospores and oospores give rise to zoospores may be correct. Flagellated zoospores obtained in this study were produced by oospores which were isolated from the bottom of a general collection dish. Aplanospores were the products of oospores obtained from females which had been isolated from a general collection and had been allowed to mature

and release their eggs in separate culture dishes. This latter group had less opportunity for fertilization and thus parthenospores may have been formed, whereas in the former group prolonged association with other colonies provided greater opportunity for fertilization which would result in the formation of diploid oospores. At present, the evidence seems to indicate that environmental factors determine, at least to some extent, the production of aplanospores or zoospores in *V. Carteri*. Germination experiments show also that the period of ripening of oospores may be fairly brief. Ten days after healthy females were separated from a general collection, their released oospores were placed in Uspenski's fluid, where they germinated on the following day. Presumably, environmental conditions permitting, oospores ripen and germinate quickly in nature. Long resting periods may occur when oospores remain in unfavorable environments. In Zimmerman's (1921) cultures zygotes germinated after from two to three months, and were apparently unaffected by such external conditions as light and heat, although they were shielded, in part, from sunlight. Pocock (1933b) observed best germination from "oospores [of *V. Rousseletii*] placed in water obtained from *Volvox* 'vleis' [pools] and strained, placed in the sun," and "oospores placed in pond water plus a small quantity of culture medium (Uspenski and Uspenskaja 1925)." The later fluid used full strength "did not give good results, causing pathological phenomena in the developing colonies." The results of Pocock's (1933b) germination experiments on oospores of *V. Rousseletii* may be summarized as follows: 1. "Direct sunlight is necessary for the germination of the oospores." 2. "Complete drying is not essential but is beneficial." 3. "Oospores are not necessarily fully mature when liberated by the break up of the parent colony."

The present study of *V. Carteri* has shown that: (1) oospores may germinate under a combination of indirect daylight and artificial illumination; (2) only wet spores are capable of germination under the conditions provided in the experiments; (3) oospores mature and germinate rapidly (within two weeks) under conditions provided in the experiments; (4) either aplanospores or zoospores may be produced by germinating oospores according to the culture fluid used.

## INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

The Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of three cents for each card. **The different subjects as classified below may now be ordered separately** (but no orders will be taken for less than one year's issue in any classification). Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

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## A MORPHOLOGICAL AND CYTOLOGICAL STUDY OF A NEW FORM OF *VOLVOX*—II\*

JEROME METZNER

### CYTOLOGY

In a very brief description of nuclear division in *Volvox minor* (*V. aureus*) Overton (1889) reported that the nucleolus is dissolved, the nucleus swells considerably and goes into a kind of spireme condition; division is described as of the indirect type involving the formation of thread-like chromosomes. Overton found that nuclear division in developing daughter colonies is synchronous. He considered lack of many division figures as indication that division occurs quickly. None of the details of nuclear division is described.

The first intensive account of vegetative mitosis, cell division and meiosis in *Volvox* was published by Zimmerman (1921). A summary of his observations follows: Before mitosis the nucleus and its enclosed nucleolus undergo enlargement, and the latter at times becomes vacuolated. The Randkörper, a small chromatic body usually found near the nucleolus, disappears during prophase. Condensation of chromatic material occurs and progresses until 12 chromosomes are formed. Up to this point the nucleolus remains structurally unchanged, but moves toward the nuclear membrane, gradually diminishing in size, and finally disappears as it reaches the nuclear border. In metaphase centrioles are sometimes visible at the poles of the intranuclear spindle. During telophase chromatic droplets appear between the disappearing chromosomes of each daughter set. Aggregation of chromatic materials results in the reformation of nucleoli and in addition the Randkörper reappears in each daughter nucleus. Cell constriction follows nuclear division. Zimmerman remarks that nuclear division must occur rapidly because division stages were found comparatively rarely. Material fixed at 3 p.m. on January 24, 1919, showed about 2 per cent of the nuclei dividing, and this is considered especially rich. No evidence of reduction division was observed in the formation of eggs or sperm, and every division of antheridial cells showed 12 chromosomes.

After a two-month resting stage, the oospore germinates, and the first nuclear division is reductional. Twelve bivalent chromosomes are produced these form rings or tetrads in the center of the nucleus. From this point on Zimmerman admits that he does not have a complete picture of meiosis, but considers that the evidence is sufficient to warrant the conclusion that the

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zygote represents the diploid phase of the *Volvox* life cycle, and that reduction occurs during the first division of the germinating zygote nucleus. His figures seem to indicate an intact nuclear membrane throughout the mitotic cycle, although he does not mention that mitosis is intranuclear.

Studies on mitosis in *Volvox* are difficult because of the paucity of division figures. After colonies had been fixed at hourly intervals during the day and night, it was found that there were two periods of maximum mitotic activity—an optimum period, occurring at approximately 3 p.m., and another period with somewhat less activity taking place at 10 p.m. Colonies fixed at other hours of the day or night showed few or no signs of mitotic activity.

The interkinetic nucleus of an undivided gonidium (figs. 1, 98) is 13–17  $\mu$  in diameter and occupies a more or less central position within the cell. It is bounded by a definite membrane enclosing (a) a relatively large, spherical endosome, 4.5–6.7  $\mu$  in diameter, staining densely with iron-alum haematoxylin and giving a positive reaction to the Feulgen test; (b) a smaller, spherical body, 1–1.5  $\mu$  in diameter, usually located near the endosome, also staining with iron-alum haematoxylin, but reacting negatively to the Feulgen test; this nuclear element will be referred to as a plasmosome for reasons which are stated below; (c) a reticulum of delicate threads reacting with fast green counterstain; (d) occasional minute granules occurring within the meshes of the reticulum.

During interkinesis there is evidence that changes are occurring within the endosome. At times this body stains homogeneously with each of the nuclear stains used, but a process of vacuolization begins, during which, at first, numerous small clear, non-staining vacuoles are formed (figs. 2–5). As the vacuolization process continues, the smaller vacuoles seem to merge, resulting finally in an endosome with one or a few large vacuoles (figs. 3, 4). In two separate observations a pale, spherical endosomal bud was seen attached to the original endosome (fig. 90). The bud may be derived from vacuolar material, since the residual endosomal mass is non-vacuolated and smaller than non-budding, vacuolated endosomes, and the bud has the same negative staining reaction to nuclear dyes as the vacuolar material. The subsequent history of the endosomal bud could not be traced.

The onset of mitosis is usually made manifest by an accumulation of minute cytoplasmic threads, possibly mitochondria, around the nuclear membrane.

During prophase, the vacuolated endosome divides abruptly into two large, uneven masses which separate in opposite directions (figs. 6, 7, 99). This process must occur very swiftly, for few intermediate stages were observed between the splitting of the endosome and the arrival of the daughter halves at opposite poles of the nucleus (fig. 7). The endosomal substance

seems to have a high viscosity, for as the two daughter masses move apart to opposite poles, they remain connected for a time by many slender threads having numerous, bead-like condensations of endosomal material along their lengths (figs. 6, 99). These granular connecting threads disappear later, leaving two densely staining, polar endosomal masses completely separated (figs. 10-12). Frequently, endosomal division occurs in such a way that in addition to the two polar masses, smaller masses of endosomal material, one or several, become detached and remain near the center of the nucleus for a time (figs. 8-10), but disappear in later prophase.

Endosomal division followed by migration of the products to opposite poles of the nucleus usually prevails. No morphological mechanism for endosomal division could be detected. The spindle apparatus does not appear until late prophase. Infrequently, the endosome does not lie near the center of the nucleus but is eccentric. Such an endosome does not divide, but remains on the side of the nucleus even after the spindle has been formed (figs. 17, 91). There it gradually disintegrates and finally disappears.

During these early prophasic stages the plasmosome disappears completely and does not reappear until the daughter nuclei are formed. Because this body is Feulgen-negative, disappearing during prophase of mitosis and reappearing during late telophase, it seems to correspond in its general history to the plasmosome of higher plants.

Certain changes occur within the polar endosomal masses, resulting frequently in the formation of finger-like processes on the sides of the bodies facing the interior of the nucleus (figs. 8, 9). At the same time the outer portions generally begin to lose their avidity for nuclear dyes (figs. 8, 12, 106). While these changes are taking place the polar masses continue to move in their original directions and gradually push or dissolve their way through the nuclear membrane (figs. 10-13). During movement through the nuclear membrane into the cytoplasm those portions of the polar masses within the nuclear membrane stain densely with iron-alum haematoxylin especially at the inner edges, while the portions outside the nuclear membrane take only the fast green counterstain (figs. 12, 13).

Thus while extrusion is taking place chemical changes occur within the endosome. These processes continue until the polar masses are completely eliminated from the nucleus into the cytoplasm. There, at first, they are definite bodies not staining with iron-alum haematoxylin and reacting negatively to the Feulgen test. Shortly afterwards they disappear, leaving behind no trace in the cytoplasm (figs. 15, 16, 109, 110, 111). A spindle appears in the plane occupied previously by the connecting strands of the polar masses (figs. 15, 111, 112). Prophasic chromosomes showing evidence of equational division and apparently derived from elements within the nuclear reticulum, are formed (fig. 14) and arrange themselves on the equator of the spindle (fig. 100).



Because metaphase figures occur with relatively high frequency it may be assumed that this phase is retained for a longer period than some of the others. At the beginning of anaphase there may be some faint evidence of intranuclear polar masses (figs. 15, 109). Later, however, when the daughter chromosome-sets separate there is no trace of intranuclear endosomal material (fig. 16). Considerable shrinkage occurs in the chromosomes between prophase and metaphase so that at the latter stage the chromosomes are finally about  $0.5\ \mu$  or smaller in diameter, whereas formerly they were approximately  $0.75\text{--}1.0\ \mu$ . Because of their extremely small size and crowding it was impossible to determine the number of the chromosomes. In figure 14 there are 20 bodies, some of which are obviously double whereas others may or may not be so. The preceding section through the same cell contains two more bodies, giving a total of 22. However, since the slide was stained with iron-alum haematoxylin it is impossible to determine which of the bodies are chromosomes and which are endosomal fragments. None of the Feulgen-tested material had prophasic stages with large divided chromosomes, but it contained a large number of metaphases with chromosomes too minute and closely packed to permit an accurate count.

Few anaphases were observed, indicating that movement of the chromosomes from the equator of the spindle to opposite poles occurs rather quickly (figs. 15, 16, 17, 111, 112).

After the chromosomes have reached the opposite poles of the spindle (figs. 18, 113) they begin to aggregate there. A rather densely staining coarse reticulum is formed in which the identity of the separate chromosomes is lost (figs. 19, 114, 115, 118). The total amount of chromatic material seems to increase. These tendencies, aggregation of chromatic masses together with increase in total amount of chromatic material, continue until finally two large compact spherical endosomes are formed within separate nuclei (figs. 20, 119). In addition the plasmosome makes its appearance at about this time. All of these mitotic processes appear to occur within an intact nuclear membrane. Although final separation of two nuclear masses was not observed it seems probable that the nuclear membrane between the chromosome-sets constricts, and is eventually severed near the center, thus producing two nuclei within the dividing cell (figs. 116, 119). Karyokinesis definitely precedes cytokinesis, yielding a binucleate stage which is maintained for some time (figs. 20, 116, 119). Later, the cytoplasm begins to constrict in the region between the two daughter nuclei (fig. 116). Constriction continues until cytokinesis is completed. Newly formed nuclei are considerably smaller (fig. 116) than older nuclei which are about to divide. As newly formed daughter cells of young developing daughter colonies carry on their metabolic activities their nuclei increase in size and may reach about  $17\ \mu$  before undergoing mitosis.

Mitosis in *V. Carteri* is intranuclear and it seems likely that this condition also obtains in *V. aureus* (Zimmerman 1921). Both species have similar resting vegetative cell nuclei each possessing a large endosome and an additional body called a Randkörper by Zimmerman, but interpreted in this paper as a plasmosome. In each species this body disappears during the prophase of mitosis. On the basis of certain microchemical tests Zimmerman (1921) held that the nucleolus of *V. aureus* was similar to that of higher plants. However, the Feulgen test (Feulgen & Rossenbeck 1924) was not available at that time and relatively little was known of the nucleic acid content of nuclear elements or of the cytoplasm. Beyond the similarities already indicated between the vegetative cell nuclei of *V. Carteri* and *V. aureus* there are few additional ones once division begins. Endosomal division, characteristic of cell division in *V. Carteri* does not occur in *V. aureus*; nor does Zimmerman report nucleolar budding or extrusion. In *V. aureus*, he observed centrioles at the poles of many metaphase spindles, but they could not be identified with certainty in *V. Carteri*. The latter species has minute granular chromosomes of indeterminate number whereas in *V. aureus*, the chromosomes are considerably larger and thread-like.

Thus there are several outstanding differences in the mitotic cycle of these two species of the genus *Volvox*.

Since it has been impossible, thus far, to secure division figures in germinating oospores of *V. Carteri* no statement can be made concerning any changes in chromosome number which may occur. However, the fact that some germinating oospores were found containing from two to four nuclei, is at least suggestive of the possibility that in some oospores meiosis takes place. Moreover, the large number of germinating oospores having single nuclei, together with the evidence previously presented in this paper, also suggests that these uninucleate germinating oospores are haploid parthenospores. Pocock (1933b) also observed a few oospores with their contents divided into four and states that in germination of the oospore reduction probably takes place.

Among the protista intranuclear mitosis, involving a large nucleolus-like body, is common. Wilson (1925) and Sharp (1934) mention many examples of this type of mitosis. Wilson (1925) states that in such cases "an intranuclear spindle is formed by elongation and ultimate division of the karyosome." "The poles of the spindle in typical cases are occupied by deeply staining 'polar masses' or 'polar caps' derived directly or indirectly by division of the karyosome. The spindle itself appears to be formed in some cases entirely from the karyosome, in other cases in part at least from the linin substance of the peripheral nuclear zone surrounding the karyosomes." In its broad features this description of protistan mitosis characterizes mitosis in *V. Carteri*, but bears little relation to the mitotic cycle of *V. aureus* de-

scribed by Zimmerman (1921). The extrusion of the endosome-derived polar masses into the cytoplasm is an unusual additional feature of mitosis in *V. Carteri*. Concerning the mechanism responsible for division of the endosome and the origin of the spindle, little can be said on the basis of actual observation. It is possible that division of the endosome is autonomous. Progressive vacuolization in this body indicates that it is not a passive nuclear structure. The endosome may function as a centriole or contain within it a centriole although no evidence of such a structure could be detected by any staining technic. There is also the possibility that a physico-chemically differentiated, but morphologically undifferentiated spindle apparatus is responsible for the rapid division of the endosome into polar masses. That this region usually develops near the central axis of the nucleus is indicated by those nuclei in which the endosome is situated eccentrically. Under these conditions the endosome is not divided but remains on the side of the spindle which is formed later. Finally, there is the possibility that formation of polar masses is due to a combination of the two forces indicated above, namely, autonomous division of the endosome together with the presence of an invisible, but functional spindle mechanism.

Superficially it would appear that the connecting strands between the polar masses become converted into the spindle mechanism. However these threads stain with iron-alum haematoxylin, are granular, and seem to disappear. Shortly afterwards a typical spindle appears in the same plane as the connecting strands. If the possibility suggested above is true, this spindle apparatus has been present in the nucleus from the beginning of mitosis. It may be responsible for endosomal division resulting in the formation of polar masses and their connecting threads. Then this hitherto invisible mechanism becomes morphologically differentiated into an orthodox spindle.

Frew and Bowen (1929), describing mitosis in a cucurbit, show that the accidental location of the nucleolus in the spindle area results in the elongation of the nucleolus with its long axis parallel to that of the developing spindle and finally its separation into two masses. Normally in the cells of the cucurbit the nucleolus is to one side of the developing spindle and there undergoes dissolution. This condition is similar in some respects to that which obtains in *V. Carteri*, in which the endosome usually is caught in the spindle area and divided, but when the endosome is at one side it remains undivided and undergoes gradual dissolution. In each case the determining factor of nucleolar or endosomal division is occurrence of these bodies in the spindle area—fortuitously or normally.

Nucleolar extrusion in animals correlated with the elaboration of cytoplasmic products such as yolk and fat has been summarized recently by Gates (1942). Except in certain fungi, nucleolar division and extrusion among the protista are not common.

It is generally recognized on the basis of Feulgen staining that the nucleoli (plasmosomes) or related structures of most plant and animal cells do not contain chromatin. However, a few organisms in which such bodies have been found to be Feulgen-positive are cited by Gates; e.g., the nucleolus in the egg of *Stegomyia* and the periphery of the nucleolus of *Anopheles* (Bauer 1933). In *Ceratomyxa* Noble (1941) finds that the karyosome is Feulgen-positive. Thus, although the number of cases is relatively few, there is definite evidence that some nucleoli or related structures are Feulgen-positive, which indicates that they contain desoxyribose nucleic acid.

White (1942), summarizing the research of the principal workers in the field of nuclear chemistry, states some of the known facts concerning nucleic acids as follows: "Nucleic acids are polymers of nucleotides each nucleotide being composed of one molecule of phosphoric acid, a pentose sugar and a purine or pyrimidine ring. The various kinds of nucleotides have different purines or pyrimidines. Apart from this there are two main types of nucleotides which differ in the nature of the pentose. In one type the sugar is d-ribose while in the other it is desoxyribose. The Feulgen reaction depends on the Schiff reaction for aldehydes which is given by the desoxy—but not by the ribose sugars."

Caspersson (1936, 1940) developed an ultra-violet absorption technic for detecting nucleic acids, and using this method, demonstrated the presence of large quantities of nucleic acids in the nucleus and cytoplasm of cells about to undergo rapid division. A region that strongly absorbs ultra-violet light at 2600 Å is assumed by Caspersson to contain nucleic acid. If it is Feulgen-positive the nucleic acid is assumed to be the desoxyribose type. If Feulgen-negative it is considered to be the ribose type. Extensive studies by the Caspersson school have shown that nuclear chromatin is always rich in desoxyribose nucleic acid; while the nucleic acid of the cytoplasm is of the ribose type. It has been established that true nucleoli (plasmosomes) contain ribose nucleotides, and it is believed that they may represent temporary storage places for nucleic acid. Because of these important differences in distribution of the two nucleic acids it has been suggested recently that desoxyribose nucleic acid be called chromonucleic acid and that the ribose form be called plasmonucleic acid (Pollister and Mirsky 1943).

There have been several observations which suggest that the nucleic acids may change their position from nucleus to cytoplasm (Schultz 1941) or vice versa (Painter 1943) with a coincident alteration to the type of nucleic acid characteristic of the new location. By analogy with these when a Feulgen-positive material goes from the nucleus to the cytoplasm and there becomes Feulgen-negative there is ground for the assumption that this involves the conversion of a nuclear chromonucleic acid to its cytoplasmic counterpart, plasmonucleic acid.

In *V. Carteri* a Feulgen-positive endosome is divided into two polar masses, each Feulgen-positive, which are extruded into the cytoplasm, and there become Feulgen-negative and ultimately lose their identity. Only a few division figures showing the extruded polar masses in the cytoplasm have been found. However the history of the endosomal masses presented above suggests that desoxyribose nucleic acid stored in the massive endosome is extruded into the cytoplasm and there undergoes a change to some other substance—possibly plasmonucleic acid. It is difficult to speculate on the function of the extruded nucleic acid in the cytoplasm except to suggest a possible role in the elaboration of cytoplasmic storage materials found in abundance in the cells of developing colonies (Schultz 1941).

The difficulties experienced by Overton (1889) and Zimmerman (1921) in finding division figures were also shared by the writer. Although two daily periods of maximum division were found, the percentage of division figures was far less than the 2% found by Zimmerman.

Synchronization of division observed by Overton and Zimmerman in other species also occurs in *V. Carteri*, even up to well advanced stages in the development of daughter colonies.

#### TAXONOMIC CONSIDERATIONS

After the discovery of *Volvox* by Leeuwenhoek (1700), two species, *V. globator* and *V. aureus*, became known in both the Old and New Worlds. Further studies increased the number of known species to ten according to Pascher (1927) and seventeen according to Printz (1927). New species and several forms of some of these species have been described since these reviews, so that some 15–20 species of *Volvox* are known to date. In the United States the following species have been reported up to the present time:

With protoplasmic connections: *V. globator* (L.) Ehrenberg, *V. perglobator* Powers, *V. aureus* Ehrenberg.

Without protoplasmic connections: *V. Weismannia* Powers, *V. spermatosphaera* Powers, *V. mononae* Smith.

Carter (1859) found a species of *Volvox* in Bombay, India, which he erroneously called *Volvox globator*. After reading Carter's account, Stein (1878) corrected the error by renaming the species *Volvox Carteri*. Powers (1908) described three new species of *Volvox* from Nebraska, including *V. Weismannia*. Various Philippine forms of *Volvox*, including *Volvox Carteri* var. *Manilana*, were reported by Shaw (1919, 1922a, b, c). He pointed out that the strong similarities existing between *V. Carteri* and *V. Weismannia* warranted their inclusion in one species. *V. Weismannia* became *V. Carteri* var. *Weismannia*. Printz (1927), summarizing the genus *Volvox* in Engler's "Die natürlichen Pflanzenfamilien," placed *V. Carteri* in the *Merrillo-sphaera* section of the genus, and, in addition, followed Shaw by including

*V. Weismannia* as a variety of *V. Carteri*. Pascher (1927) stated that *V. Weismannia* was an uncertain species which Shaw included with *V. Carteri*—itself a very inadequately known form. Playfair (1918) found *V. Carteri* in algal collections made in Australia. The type form of *V. Carteri* as well as *V. Carteri* f. *nagariensis* were reported by Iyengar (1933) from Madras, India. Apte (1936) observed some species of *Volvox* including *V. Carteri* from Poona, India. A new variety of the species was not created, although his description seems to warrant it. The close relationships as well as the differences between *V. Carteri* and *V. tertius* are indicated by Pocock (1938) in her paper on the latter species. Thus *V. Carteri* has been found in India, the Philippine Islands, Australia, and in Nebraska.

In the summers of 1941, 1942, and 1943 the writer collected *Volvox Carteri* from aquatic plant tanks at Saddle River, Bergen County, New Jersey. This form of *Volvox* was available from early May to September in enormous quantities, free from other species of *Volvox*. Certain constant minor variations in size of the coenobia and oospores, membrane structure, and particularly the number of oogonia and sperm platelets observed over a period of three years seem to be sufficient to distinguish *Volvox Carteri* var. *Hazeni*,<sup>3</sup> the distinguishing characteristics of which are as follows:

*Volvox Carteri* var. *Hazeni* Metzner, var. nov. Coloniae vegetativae 500–756  $\mu \times$  500–785  $\mu$  metientes, e 4000–5000 cellulis globosis vel ellipsoidalibus vel leviter ovoideis constitutae; membrana communi protoplasmata e globosis ad ellipsoidalia a filis non nectata prope peripheriam claudenti; quaque cellula in prismatic 5–7-laterali gelatinoso conclusa membrana exteriori convexa interiorique leviter orbiculata munito. Propagatio asexualis pro more 8 colonias filiales configendo, eorum cellulis sexualibus cum 64 cellulae adsunt distinctis atque mensuram magnam ante divisione attingentibus; cellulae sexualis protoplasmate in membrana presse adhaerenti et in prismatis membrana ab eo leviter separata concluso; coenobii cavea materia alveolata gelatinosa atque cellulorum vegetativorum sexualiumque membranis prismaticis expleta.

Coloniae sexuales rigide heterothallicae; coloniis parvis masculinis 242–357  $\mu \times$  257–364  $\mu$  metientibus e 600–1100 cellulis constitutis quorum circa 50 discos antherozoidiorum leviter cupuliformes facientibus; disco plerumque 128 antherozoidia foveanti post coloniam masculinam e coenobia parentali expulsam maturescentia; coloniis femineis maturis 371–671  $\mu \times$  392–678  $\mu$  metientibus quam coloniis asexualibus maturis majoribus e 3500–4000 cellulis constitutis; colonia 18–20 oosphaeras foveanti ut oosporas maturescentes exospora reticulata munitas atque protoplasmata centralia in maturitate fulva habentes; aplanosporis vel zoosporis biflagellatis ex oosporis germinantibus orientibus.

Coloniae parentales colonias asexuales, masculinas, femineasve vel harum combinationes capientes, at masculinis femineisque nunquam in eadem colonia parentali praesentibus.

<sup>3</sup> In honor of the late Professor Tracy E. Hazen.

In his description of *V. Carteri* Carter (1859) pointed out that male coenobia contained about 100 sperm platelets and that female colonies contained 30–50 eggs. In *V. Carteri* var. *Hazeni* male coenobia have about 50 sperm platelets and there are usually 18–20 eggs in the female coenobia. These are the major distinguishing features of the new variety.

A chart summarizing the pertinent data published by those who have worked with *V. Carteri* has been constructed to include, under selected categories, similar information on *V. Carteri* var. *Hazeni*. Data on the other species of the section *Merrillosphaera* have been included for comparison. Blank spaces in the table represent gaps in the knowledge of these forms (Plate 1).

A diagram representing the life cycle of *V. Carteri* var. *Hazeni*, as described in this account, is included (fig. 120).

#### Summary of Numerical Data

Asexual colony	500 $\mu$ to 756 $\mu$ $\times$ 500 $\mu$ to 758 $\mu$
Sexual colony, male	242 $\mu$ to 357 $\mu$ $\times$ 257 $\mu$ to 364 $\mu$
Sexual colony, female	371 $\mu$ to 671 $\mu$ $\times$ 392 $\mu$ to 678 $\mu$
Somatic protoplast, median optical view	6.7 $\mu$ to 8.3 $\mu$
Length of flagella	21.7 $\mu$ to 23.4 $\mu$
Asexual colony, just before birth	207 $\mu$ to 236 $\mu$ $\times$ 214 $\mu$ to 243 $\mu$
Male colony, just before birth	228 $\mu$ to 257 $\mu$ $\times$ 235 $\mu$ to 263 $\mu$
Female colony, just before birth	207 $\mu$ to 236 $\mu$ $\times$ 214 $\mu$ to 243 $\mu$
Gonidium, before dividing	about 80 $\mu$
Egg	48 $\mu$
Oospore	about 54 $\mu$ ; 46–60 $\mu$
Protoplast of oospore	about 45 $\mu$
Number of cells, asexual colony	4000–5000
Number of cells, male colony	600–1100
Number of cells, female colony	3500–4000
Number of daughter colonies	characteristically 8
Number of oospores	18–20
Number of sperm platelets	about 50
Sperm platelet	30 $\mu$ to 33.4 $\mu$ $\times$ 11.6 $\mu$ to 14.1 $\mu$
Number of spermatozooids per platelet	128
Attachment of flagella on spermatozooids	terminal

Various criteria for distinguishing *Volvox* species have been established by different workers throughout the world. Meyer (1896) showed that the internal structure and membranes of *Volvox* colonies, as revealed by his methylene blue technic, were features which could be used together with the more familiar ones in distinguishing *Volvox* species. Shaw (1922a, b, c) thought that membrane and internal structure of *Volvox* colonies stained by Meyer's technic, along with the following additional features, were important: 1. Presence or absence of protoplasmic connections; 2. The stage at which the gonidia differentiate. However, Pascher (1927) states that differences among *Volvox* species such as the stage of differentiation of gonidia depend, to a large extent, on external conditions and thus do not have universal application. He believes that metabolic rate, temperature, and pH play the greatest role in determining certain structural and developmental features of *Volvox* and he has developed a theory of the polyphyletic origin





[illegible]

**MERZNER: VOLVO**



of the genus based largely on a consideration of the cell and colony membrane structure. Iyengar (1933) considers that apart from cell structure the following criteria are fundamental in taxonomic considerations: 1. The distribution of the sexes; 2. The numbers of reproductive cells; 3. The disposition of the gonidia; 4. The character of the oospore. Pocock (1938) lays great stress on membrane structure as a basis for specific segregation in *Volvox*.

Most of the recent workers agree that an application of methods such as those of Meyer (1896) to a study of the details of cell structure and internal anatomy is essential for a clearer understanding of the taxonomic relationships in the genus *Volvox*. Most of the criteria stressed by various workers seem to be valid. Further comparative studies especially on the germination of the oospore and cytological analysis of various *Volvox* species will undoubtedly provide additional useful criteria.

The differences existing among species of *Volvox* seemed great enough to Shaw (1922a) to warrant their separation into different genera. Shaw's ideas on the reclassification of *Volvox* were incorporated in Printz' (1927) treatment in which, however, Shaw's generic names were given to sections of the one genus, *Volvox*. It is interesting to note that Printz included the section *Campbellosphaera* containing *Volvox obversus* (Shaw) Printz. Pascher (1927) and Iyengar (1933) recognize Shaw's error in distinguishing this form of *Volvox* as a separate species. In the opinion of Iyengar (1933) and Smith<sup>4</sup> (1933) the establishment of separate genera by Shaw seems unwarranted. Fritsch (1935), Pocock (1933), and Pascher (1927), however, have tentatively accepted Printz' treatment of the genus pending further investigations.

Inversion in *Volvox* was first noted by Powers (1908) and later described, in detail, by Kuschakewitch (1922), Zimmerman (1925) and most completely by Pocock (1933b, 1938). Since Shaw (1919) was apparently unaware of the inversion process in *Volvox* he incorrectly established the genus *Campbellosphaera* based on features which are now recognized as inversion phenomena. In view of these considerations it is apparent that the section *Campbellosphaera* of the genus *Volvox* is unwarranted and the form described by Shaw as *Campbellosphaera obversa* should be renamed and placed in its proper taxonomic position, namely, as a variety of *Volvox Carteri*.

It becomes evident, after a review of the more important taxonomic literature on *Volvox*, that a revision of the genus is needed. The acceptance, by several of the more recent workers, of Printz' division of the genus into sections indicates that this treatment has merit. In the writer's opinion it is a convenient device which can be improved as further investigations on all species of *Volvox* establish sound diagnostic features for each section.

<sup>4</sup> Smith, however, incorrectly states that *V. Weismannia* Powers possesses stout protoplasmic connections.

Printz (1927) characterizes the section *Merrillosphaera* as follows: protoplast spherical-egg shaped, lacking protoplasmic connections; gonidia developed early in ontogeny and reaching a good size before cell division is initiated. All descriptions of the species of *Volvox* included in the section mention these features and therefore the section *Merrillosphaera* seems to have some validity. Printz included in the section *V. africana* West, *V. Carteri* Stein [= *Merrillosphaera Carteri* (Stein) Shaw incl. *V. Weismannia*], *V. Migulae* (Shaw) Printz, *V. tertius* Meyer, and *V. mononae* Smith.

Pocock (1938) believes that *V. Migulae* is identical with *V. tertius*, and both she and Pascher (1927) agree that *V. mononae* is not a good species.

It seems advisable to abandon *V. mononae* (Smith 1920) as a species of *Volvox* and to allocate *V. Migulae* to the position indicated by Pocock (1938), namely to *V. tertius*.

*V. gigas* from Kimberley, Africa, was placed in the section *Merrillosphaera* by Pocock (1933b).

In summary, therefore, the following revision of Printz' (1927) classification of the genus *Volvox* is suggested. 1. The inclusion of the following species in the section *Merrillosphaera* of the genus *Volvox*: *V. Carteri* Stein, *V. tertius* Meyer, *V. africanus* West, *V. gigas* Pocock. 2. The elimination of the section *Campbello-sphaera*.

It was pointed out by Shaw (1919) in his description of *Campbello-sphaera obversa* that this form of *Volvox* closely resembled *V. Carteri* and *V. tertius*. As indicated in Plate 1, the essential characters of *C. obversa* correspond very closely to those of *V. Carteri* except that *C. obversa* is homothallic whereas all forms of *V. Carteri* are heterothallic. After considering the above details the writer proposes that *Campbello-sphaera obversa* be assigned to *Volvox Carteri* as *Volvox Carteri* var. **homothallicus** Metzner, var. nov. [= *Campbello-sphaera obversa* Shaw; = *Volvox obversus* (Shaw) Printz].

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#### SUMMARY

1. A study of *Volvox Carteri* var. *Hazeni*, a new variety, is presented, with emphasis upon studies of the living organism.
2. Cultures were maintained in the laboratory during the summer months in solutions to which regular additions of iron salts were made.

3. The membrane and vegetative cell structure closely resemble those of *V. tertius* Meyer. Vegetative cells of crushed coenobia may become detached and free-swimming.

4. Asexual reproduction is characteristically by production of eight daughter colonies in which the reproductive cells are differentiated at about the 64-celled stage. No protoplasmic connections were visible in the development of daughter colonies, which undergo inversion in a manner similar to that described for other species of *Volvox*.

5. In sexual reproduction, *V. Carteri* is heterothallic. Female colonies produce 18–20 eggs. Male colonies are dwarf and contain about 50 bundles of spermatozooids. Fertilization was not observed nor was the presence of spermatozooids inside a female colony ever detected. It seems probable that a large number of eggs develop parthenogenetically. The oospore wall is reticulately ridged.

6. About 90 per cent germination was secured in oospore culture experiments. It was possible to obtain germination of oospores within 10 days after their release from a female colony. Germination of the oospore results in the formation of an aplanospore or biflagellate zoospore. Either product, aplanospore or zoospore, undergoes successive divisions to form a young colony which inverts to form a juvenile colony which is distinguished by its small size, few gonidia, and brownish color.

7. Two periods of maximum mitotic activity, one at about 3 p.m. and the other at approximately 10 p.m., were observed; but mitotic figures were not abundant.

8. The cells of developing daughter colonies divide synchronously.

9. Mitotic division is of the type generally occurring among the protista. A resting nucleus of a cell in a developing daughter colony contains a large Feulgen-positive endosome, a smaller Feulgen-negative plasmosome, and a linin reticulum with chromatic granules scattered through it. In prophase the plasmosome disappears and endosomal division results in the formation of two polar endosomal masses which undergo chemical changes while being extruded through the nuclear membrane into the cytoplasm. Intranuclear endosomal masses are Feulgen-positive whereas after extrusion they are Feulgen-negative. It is suggested that there is a flow of nucleic acids from nucleus to cytoplasm wherein the desoxyribose nucleic acid derived from the endosome becomes converted to cytoplasmic ribonucleic acid. Division of the endosome may be determined by the position of that body with respect to the spindle mechanism; division may be autonomous or finally it may be due to a combination of both of these factors. If the endosome lies in the spindle region, as is usually the case, it is divided into two polar masses; however, if the endosome is to one side of the spindle it is not divided, but gradually undergoes dissolution inside the nucleus.

10. The endosome may occasionally give off buds of pale-staining substance.

11. In metaphase the chromosomes are tiny and closely grouped and the endosomal masses have almost completely disappeared. The anaphases occur quickly and in telophase aggregation of chromatic material results in the reformation of the endosome; in addition the plasmosome reappears.

12. Mitosis is intranuclear. Cytokinesis is achieved by constriction of the protoplast between the daughter nuclei.

13. The evidence suggests that most of the oospores of *V. Carteri* var. *Hazeni* are parthenospores, although the possibility that fertilization occurs is not definitely excluded.

14. A revision of the section *Merrillosphaera* of the genus *Volvox* is suggested in which the species *V. mononac* Smith is abandoned and *V. Migulae* (Shaw) Printz is incorporated within another species. It is also proposed that the section *Campbellosphaera* be abandoned and the form *Campbellosphaera obversa* be named *Volvox Carteri* var. *homothallicus*.

15. A detailed description of *V. Carteri* var. *Hazeni*, var. nov., is presented together with pertinent data on the other members of the section *Merrillosphaera*.

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## THE ANATOMY OF PEACH AND CHERRY PHLOEM<sup>1</sup>

HENRY SCHNEIDER<sup>2, 3</sup>

### INTRODUCTION

In the course of a study of the effect of the buckskin virus upon the anatomy of peach (*Prunus persica* Sieb. & Zucc.) and cherry (*P. avium* L.), little literature was found concerning the phloem of peach. The development of the primary and secondary phloem in the healthy peach was therefore studied. Some attention was also given to the secondary phloem of healthy cherry. The results of these studies are herein reported. The literature on the anatomy of the peach is discussed at appropriate places in the text.

### MATERIALS AND METHODS

Much of the material used was taken from plants grown in five-gallon cans or pots in the greenhouse. Other material was supplied by Dr. T. E. Rawlins from an experimental plot in Green Valley, Solano County, California. Part of the peach material was supplied by Dr. L. C. Cochran from his plots in Moreno Valley, Riverside County, California. For the most part the study was conducted on Orange Cling peaches on peach stock and Napoleon cherries on either Mazzard or Mahaleb stock.

To make a developmental study of the phloem of peach it was necessary to have sections of successively older parts of the stem beginning with the apical meristem. Serial cross sections of the stem tip were made to a point where elongation started. Below this point pieces were taken from the center of each successive internode and from the petioles of leaves at each node. In this way developmental stages of the shoot were obtained. Sections were also made of the phloem of older stems and of the trunk.

Only secondary growth of cherry stems was considered. The bark was taken from trunks and branches of various ages.

Three fixatives were used. Alcohol-formalin-acetic no. 1 (Rawlins 1933) caused some shrinkage but had the advantage of penetrating well, and its

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use was essential when the material was in large pieces. Karpechenkos's fixative caused some shrinkage in the cambial region but was quite satisfactory for other tissues. The least shrinkage occurred when Nemec's solution was used, but it had the disadvantage of fixing tannin-containing globules, which made photography difficult. Nemec's solution required a longer time for fixation. Cell walls stained very well, even near the apical meristem, with dilute Heidenhain's haematoxylin after the use of this fixative. In preparation for embedding in paraffin, the material was treated in a manner similar to that used by Ball (1941). However, a mixture of equal parts of cedar oil and xylene were substituted for xylene. Material embedded in celloidin was handled according to the method of Jeffrey as described by Chamberlain (1932).

Haupt's adhesive (Chamberlain 1932) was used when sections were to be stained, but Ullrich's adhesive (Johansen 1940) was found to be more satisfactory when sections were to be treated with neutral or strong acid reagents in microchemical tests. The latter adhesive is soluble in bases and does not hold sections on the slide when basic reagents are used. A number of stains were used. The method of Zimmerman (1922) was found to be satisfactory for temporary mounts. Varying proportions of aqueous solutions of 0.01 per cent azure II and 0.01 per cent basic fuchsin were mixed just before using, and the sections were treated until the desired intensity was attained. The sections were then mounted in glycerol. Serial sections of stem tips and part of the other material were mordanted with iron alum and then stained in dilute Heidenhain's haematoxylin until the walls were sufficiently dark. Counter-staining with orange G in clove oil was used to impart a yellow color to the nacr  walls of the sieve tubes and callus. Delafield's haematoxylin and safranin were used for staining some of the celloidin sections.

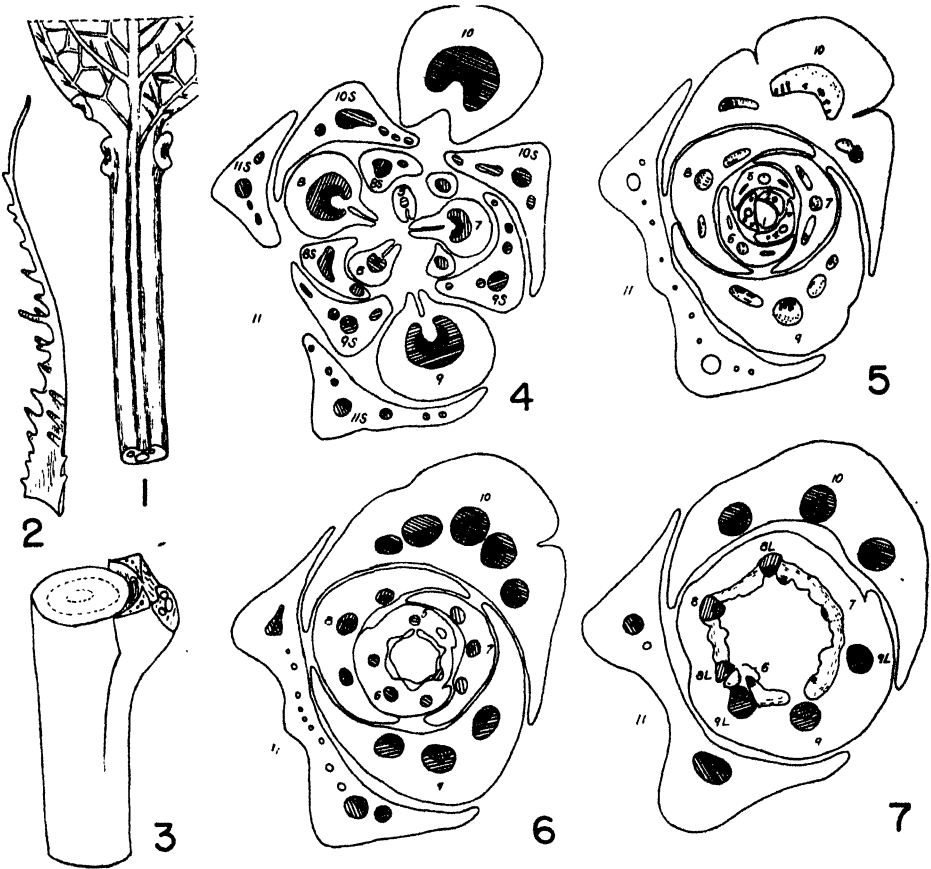
#### DEVELOPMENTAL ANATOMY OF THE PEACH PHLOEM

**General Features of the Structure and Development of the Leaf.** The leaf base partially sheaths the stem (fig. 3). The petiole of the leaf (fig. 1) is attached to the abaxial side of the leaf base in a median position. The stipules (fig. 2) are attached to the top of the leaf base.

Fitzpatrick (1934) studied the ontogeny of the peach leaf in connection with the peach-leaf-curl disease. The peach leaf appears first as a slight protuberance on the side of the apical meristem. The stipules later appear as subsidiary protuberances on both sides of this primordium. As the leaf primordium enlarges two lateral meristematic ridges appear on its adaxial face and finally develop into the leaf blade (fig. 4, leaves numbered 5, 6, 7).

With regard to the development of the peach leaf, Fitzpatrick observed the following: The glands which occur along the margins of the leaf appear and mature first at the tips of the leaves; the lateral veins differentiate first

at the apex, and the intercostal growth between the lateral veins is initiated here also; stomata first appear near the tip, and the differentiation into palisade and spongy parenchyma occurs first at the tip of the leaf, then



FIGS. 1-3. Stem, stipule, and petiole of peach. FIG. 3. Portion of a stem with a leaf base from which the stipules (fig. 2) and the petiole (fig. 1) were removed at the abscission regions. FIGS. 4-7. Cross section at several levels through a stem tip of peach. FIG. 4. 150 microns above the stem tip. Stipules appear near each side of the leaf primordia (the letter *s* indicates a stipule). FIG. 5. 50 microns below the stem tip. Dots represent sieve tubes and circles the lignified xylem elements. FIG. 6. 110 microns below the stem tip. FIG. 7. 375 microns below the stem tip. In all figures numbers represent the order of formation of the leaves, the leaf numbered 1 being the youngest. Cross hatching represents primary xylem and single hatching represents phloem. The letter *L* indicates a lateral trace.  $\times 60$ .

at the base. In other words, the peach leaf, like many other leaves, matures basipetally.

Beneath the emerging leaf primordia, groups of cells within the stem elongate in a direction parallel to the axis and thus form the procambial

strands. The cells surrounding these areas enlarge isodiametrically to form the ground meristem. The ground-meristem cells have conspicuous vacuoles and therefore their protoplasts stain less densely than the cells of the procambial strands. In an actively growing stem, the second leaf primordium had a median strand, and the third primordium had a median and two lateral strands in procambial state (fig. 5, leaves numbered 2, 3). The youngest leaf primordium at the apical cone is referred to as number one and others are numbered according to their relative ages.

Each leaf has three traces and within the stem the traces fork and anastomose with each other and form together a network in the shape of a cylinder (dictyostele). The traces of a given leaf become recognizable some distance below the node at which they diverge into a leaf (fig. 7, traces of leaf 8). The three bundles that diverged into the leaf remain unchanged throughout the lower part of the leaf base. In the upper part of the leaf base the two lateral bundles are divided (fig. 6, leaf base 10). In the basal part of the petiole proper the inner branches of the two lateral bundles are united with the median bundle and this composite bundle continues through the rest of the petiole and the midrib (figs. 4, 5, leaf base 10). The outer branches of the laterals are stipular bundles.

**Nomenclature Used and Characteristics of the Sieve Tubes.** The nomenclature outlined by Esau (1938, 1939) for the description of the different stages of development of the phloem is followed in this paper. The part of the primary phloem which matures before the stem has ceased to elongate is termed the *protophloem*. In peach the sieve tubes of the protophloem, as seen in cross section, were of approximately the same diameter as the adjacent parenchyma and procambial cells (fig. 8). In paraffin sections the walls of protophloem sieve tubes were slightly thicker than those of the adjacent parenchyma cells. The mature sieve tubes had only thin parietal cytoplasm and appeared to lack nuclei. Companion cells, if present, were indistinguishable from other parenchyma cells. Sieve plates were observed in the protophloem sieve tubes.

The primary phloem which matures after stem elongation ceases is termed *metaphloem*. The sieve tubes of the metaphloem in peach were found to be larger than the adjacent parenchyma cells and showed very thick crenulated walls with a pearly luster. This type of sieve-tube wall has been described as "nacr  " in the literature (Les  ge 1891, as cited by Esau 1939). The nacr   walls stained more lightly than the original procambial walls and the parenchyma-cell walls with Heidenhain's haematoxylin (figs. 15, 16). Companion cells were associated with the metaphloem sieve tubes. No sharp line of demarcation between the metaphloem and the protophloem was observed.

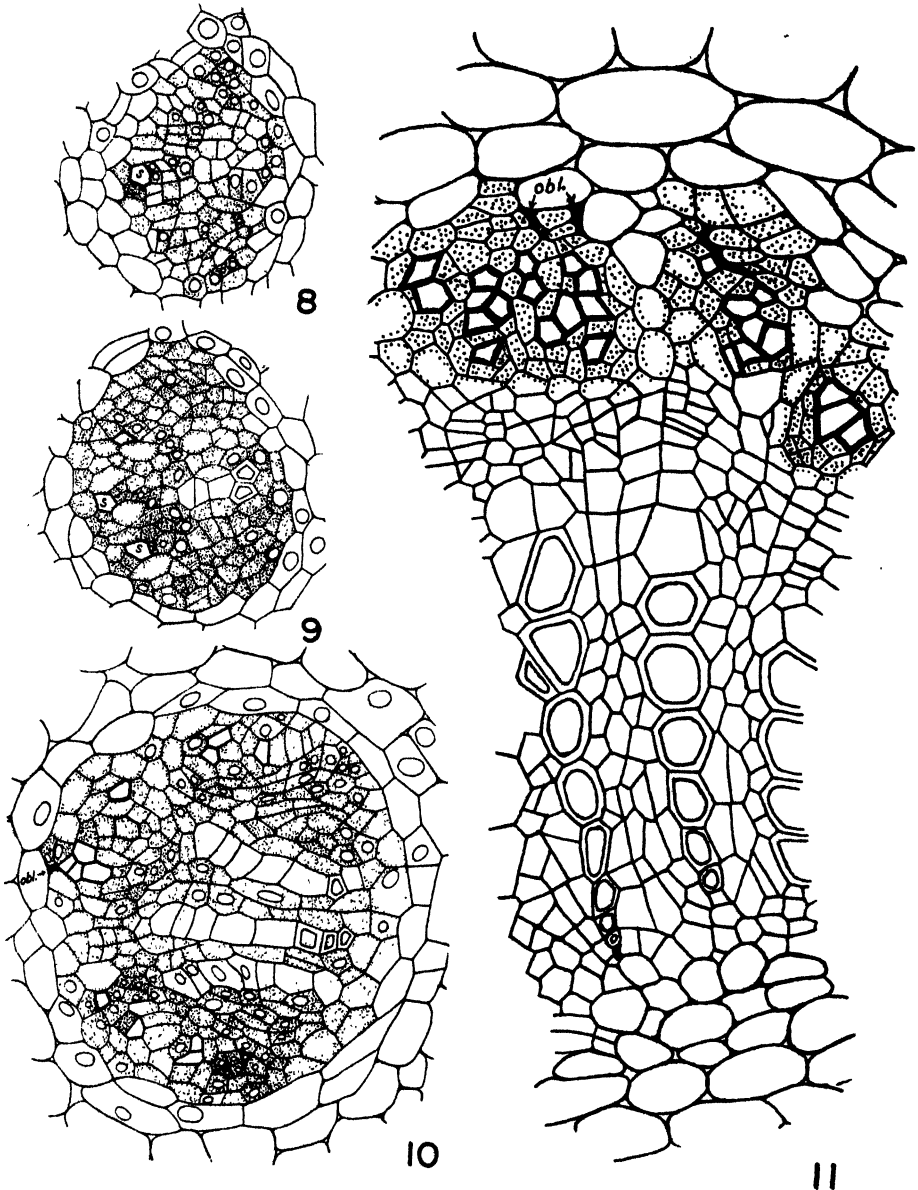
The phloem tissues initiated from the cambium are termed *secondary phloem*. As seen in cross sections of peach stems, the procambium is composed of cells polygonal in shape and periclinal divisions predominate in it. The procambium is confined to the primary bundles (fig. 12); whereas the cambium, except in early stages of transformation from procambium to cambium, forms a continuous cylinder of cells. The cambium cells are rectangular and divide in an orderly manner by periclinal walls during the formation of xylem and phloem. As seen in tangential section the cambial cells which initiate the vascular rays are about twice as long as wide and the initials which give rise to the longitudinal system are long fusiform cells.

**Ontogeny of the Phloem Tissue of the Leaves.** The study of the development of the phloem was begun by finding the youngest leaf base which

TABLE 1. *Relative age of the leaf primordium and differentiation of the first vascular elements.*

Stem tip number	The number of the leaf with the first				Nature of growth of stem
	Sieve tubes in the leaf base	Thick-walled xylem element in the leaf base	Phloem obliteration in the leaf base	Thick-walled xylem element in the petiole	
1	5	6	8	5	Rapid
2	5	8			Slowing down
3	5	5	7	5	Rapid
4	5	6	9	5	Rapid
5	6	8	8	8	Growth stopped

had a sieve tube in the median trace. Then the phloem of median bundles of successively older leaf bases was examined to determine where the next sieve tubes were formed in relation to the first and what the destiny of the first-formed sieve tubes was. The smallest leaf primordium at the apical cone is referred to as leaf number one, and the others are numbered consecutively according to their relative ages. A section 50 microns below the stem tip of a rapidly growing shoot showed that the median bundle of leaf base number 5 was the first to have a sieve tube (figs. 5, 8). This seems to be typical (table 1). The first sieve tube is initiated in the center of the abaxial margin of the bundle. No xylem elements were present at this level; however, one was present in the petiole region above. Leaf base number 6 had three sieve tubes, two additional sieve tubes having differentiated tangentially on either side of the first sieve tube (figs. 5, 9). Two lignified immature xylem elements had developed in the center of the adaxial side of the bundle. Adjacent vacuolated cells on the abaxial side of these elements were arranged in radial rows as though they were initiated from meristematic cells by periclinal divisions



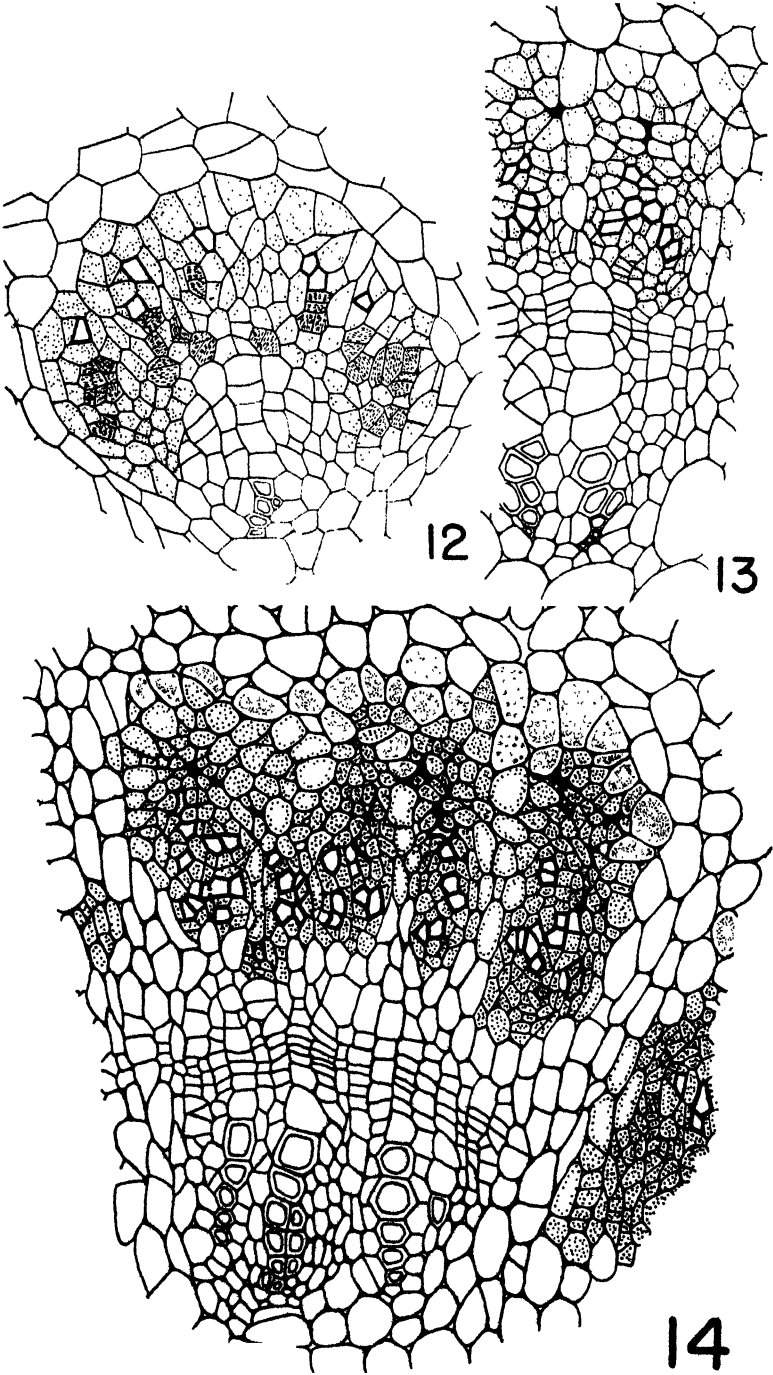
Cross sections through median bundles of leaf bases of peach. FIG. 8. From leaf base number 5. FIG. 9. From leaf base number 6. Figures 8 and 9 are 50 microns below the stem tip. FIG. 10. Bundle from leaf base number 8, 110 microns below the stem tip. FIG. 11. Portion of a bundle from leaf base number 14, 6 mm. from the stem tip. Stippled cells indicate the procambium, primary xylem and primary phloem in figures 8, 9, and 10, but only the primary phloem in figure 11. Areas inked solid or single hatched areas between cells represent obliterated phloem (*obl.*). Stippled cells with thick walls represent immature sieve tubes. Thick walled cells not stippled represent mature sieve tubes (*s*). All  $\times 650$ .

(fig. 9). They were vessel initials. At this stage the phloem region also showed a tendency toward radial arrangement of cells.

The first sieve tube was found to be obliterated in the seventh to ninth leaf bases (table 1). In the median bundle of leaf base number 8 of one stem studied, obliteration of the first sieve tube had occurred (fig. 10). New sieve tubes had differentiated along the abaxial margin of the trace and centripetal to them. In this trace the phloem was becoming divided into strands by enlargement of rows of parenchyma cells which are the beginnings of the primary rays. In the same stem in the median bundle of leaf base number 14, (fig. 11), 6 mm. from the stem tip, several sieve tubes were obliterated and new ones had arisen in a centripetal direction. The phloem region had been definitely divided into separate strands by the primary rays.

The metaphloem remains in a functioning state throughout the life of the leaf. In the differentiation of the petiole the last cells of the procambium to be initiated on the phloem side develop into large parenchyma cells which separate the primary and secondary phloem (Schneider 1945, photomicrographs of petiole sections). Only a small amount of secondary phloem is produced in the petiole and midrib of leaves. As seen in a radial section in an old leaf, the cells of the cortex which border the protophloem bundles vary from isodiametric to rectangular. The protophloem cells which remain intact after the obliteration of the sieve tubes become much elongated (1–1.5 mm. in length) and increase in cross-sectional diameter. Similar cells in the stem lay down secondary walls which become lignified. The metaphloem contains sieve tubes, companion cells and phloem parenchyma cells. In radial section the parenchyma cells are variously shaped elongated cells and the sieve tube elements are also elongated and variously curved. The parenchyma cells separating the primary and secondary phloem are from cubical to isodiametric. The phloem tissue of the lateral veins is similar to that of the midrib and petiole except that only a few strands of primary phloem are present and no secondary phloem is produced. The protophloem is obliterated in the same manner as in the petiole.

**Ontogeny of the Phloem in the Stem.** In early stages the traces of the stem develop similarly to those of the leaf. The first sieve tube appears just inside a row of cells that constitute the outermost portion of the procambial strand. The next sieve tubes develop in a tangential direction on both sides of this first sieve tube (fig. 12). The first sieve tubes are then obliterated as new ones differentiate in centripetal direction (figs. 13, 14). At this stage of development primary rays divide the primary phloem into strands (figs. 13, 14). When branching of traces occurs at certain levels of the stem, the primary rays become wider to form the leaf gaps. This occurs above the point where other leaf bundles enter the vascular cylinder. As the protophloem





sieve tubes are obliterated fibers differentiate (fig. 15). The origin of fibers is described below. Centrally to the fibers there is a region of sieve-tube obliteration and then a region of metaphloem.

Fibers of the primary bundles arise from procambial cells which did not differentiate into sieve tubes. These procambial cells elongate, increase in diameter, lay down secondary walls, and finally become lignified. Because of their procambial origin these fibers are here termed primary-phloem fibers. Until recently (Esau 1938, 1943), primary-phloem fibers have been generally interpreted as pericyclic fibers (Eames & McDaniels 1925; Hayward 1938). The fibers of the outer row have different characteristics from the other primary fibers throughout their development; they enlarge first (fig. 12), their lumina are filled with a heavily staining substance (fig. 14), they become larger and are lignified later than the subjacent fibers (fig. 15).

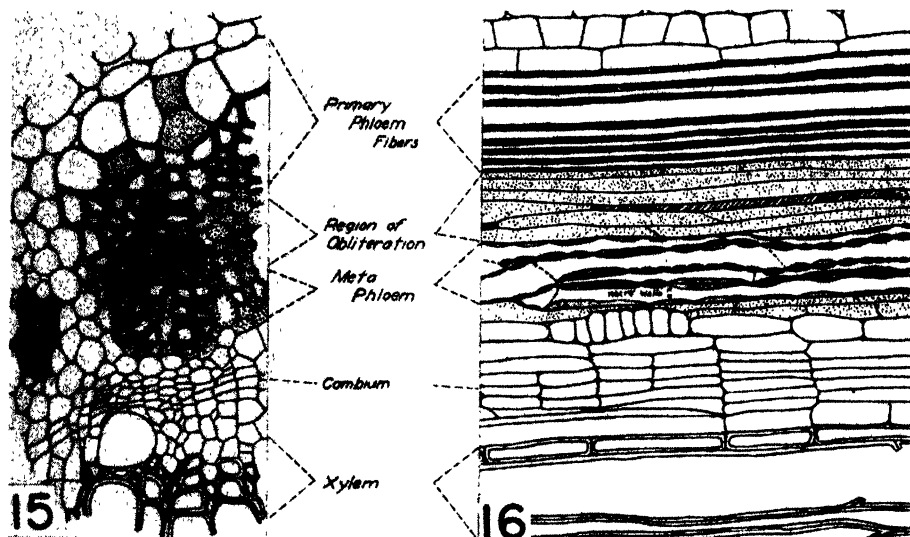
The strands of primary phloem eventually become bordered on their inner sides by large parenchyma cells initiated by the procambium after the full complement of the primary phloem mother cells are formed. Primary xylem initials are laid down more slowly than initials of the phloem until the full complement of primary phloem cells is formed. (Compare the median trace of leaf number 7 in fig. 12 with that of leaf number 9 in fig. 13.) The strands become elliptical in shape because of the tendency of the phloem mother cells to divide periclinally with respect to strands; and because of the manner in which the primary rays broaden out (fig. 14).

Partly developed primary-phloem strands are distinctly isolated from each other; and as seen in transverse sections, they appear to be meristematic on their inner sides because of the presence of small cells which contain dense protoplasm. A study of successively older traces explains how these strands are isolated and why they appear to be meristematic on their inner sides. After having been added to the strands by divisions of the procambium, most of the new phloem cells (the phloem mother cells) divide again to form the young sieve tubes, companion cells, and phloem parenchyma cells. Because of these divisions the young phloem cells appear smaller than the

#### Explanation of figures 12-14

Transverse sections of leaf traces from the peach stem. FIG. 12. Median trace from leaf number 8, 240 microns from the stem tip ( $\times 800$ ). Sparsely stippled cells represent primary phloem and procambium cells. Cells with dashes represent those that arose from the most recent divisions. Those nearest the unstippled xylem area belong to the procambium and others are recently divided phloem-mother cells. FIG. 13. Median trace from leaf number 9, 2400 microns from the stem tip ( $\times 400$ ). Figures 12 and 13 are drawn from sections from the same stems as the drawings in figures 4-11. These sections were taken from a rapidly growing stem. FIG. 14. A lateral trace of leaf 11 about 700 microns from the tip of a stem which was growing slowly ( $\times 400$ ). In figures 13 and 14 stippled cells belong to the phloem strands. Finely stippled cells contained copious precipitates, and represent immature primary-phloem fibers. Thick-walled cells represent sieve tubes. Single hatched areas represent obliterated sieve tubes.

procambial cells from which they were derived. The sieve tubes of this part of the phloem mature slowly and increase in length before they increase in diameter. Because of the slow maturation this part of the phloem remains meristematic in appearance for a considerable time (fig. 14). While the inner sides of strands are maturing into the metaphloem, the initiation of xylem becomes more active and the procambium is transformed into the cambium, which at first only gives rise to xylem (figs. 14, 15). After a considerable



Sections from peach stems. FIG. 15. Transverse section of part of the primary phloem of the middle trace of leaf number 13, just below the level where it anastomoses with the vascular cylinder, and 7.5 mm. from the stem tip. FIG. 16. A bundle of about the same age in radial longitudinal section. Both  $\times 380$ . In both figures sparsely stippled cells represent phloem parenchyma and companion cells. Single hatched areas between cells represent crushed sieve tubes and companion cells. Cells with shaded crenulated walls are sieve tube elements. Cells with thick shaded secondary walls which are not crenulated are primary phloem fibers. Densely stippled cells represent immature primary phloem fibers with vacuolar precipitates. Other large cells in figure 15 which border the outer side of the fibers are immature primary-phloem fiber initials from which the heavy precipitates were lost in preparing the sections. This outer row of fibers lays down secondary walls later than those just centrally to it.

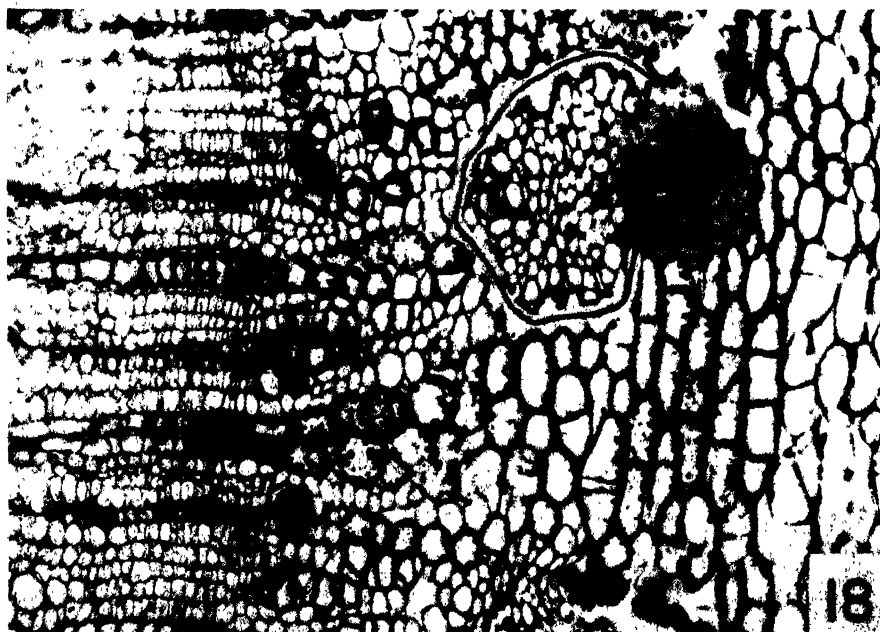
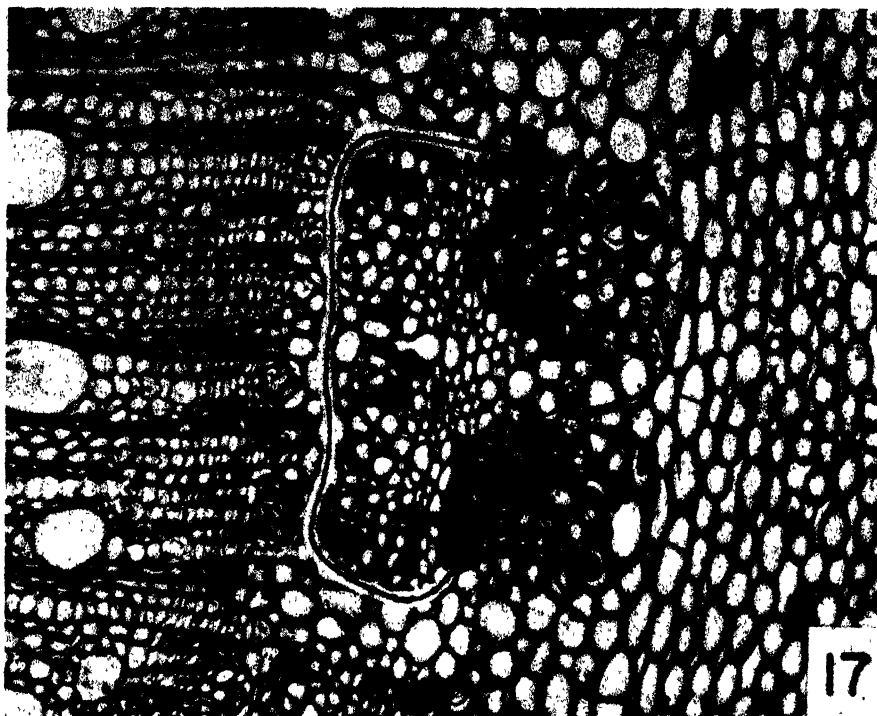
amount of xylem has been produced, the secondary phloem begins to be formed (fig. 17).

In a growing stem 32 cm. from the stem tip, secondary phloem was being produced. The secondary sieve tubes had thick nacré walls, and the nacré walls of some of the metaphloem sieve tubes had disappeared (fig. 17). A row of parenchyma cells (the origin of which was previously described) separated the primary phloem from the secondary phloem (fig. 17). Eames and McDaniels (1925, p. 107) picture a magnolia stem in which the primary and

secondary phloem are similarly separated. At certain levels the secondary and primary phloem anastomosed with each other. In the same stem 85 cm. from the stem tip, more secondary phloem had been produced and most of the sieve tubes of the primary phloem were obliterated (fig. 18). The nacre walls of the secondary sieve tubes stood out very distinctly. The walls of the primary-phloem fibers had thickened and were difficult to cut.

When a peach shoot ceases to grow, the apical cone becomes obtuse, and is sheathed by large fleshy leaf bases. A leaf trace within the stem from any given leaf may be in various stages of development depending on the nature of the growth of the stem. The median traces from leaf number 13 of two rapidly growing stems were observed to have their full complement of primary phloem cells and secondary walls were just beginning to be laid down in the primary-phloem fibers. In the primary phloem of the median trace of leaf number 13 of a stem in which growth had nearly stopped, the full complement of cells was present, and the secondary walls of the primary-phloem fibers were almost completely laid down (fig. 15). In a stem which had not produced apical growth for several weeks the fibers were completely lignified in the median trace of leaf number 13, much of the metaphloem was still functioning, and some active secondary phloem was present. The phloem of traces of younger leaf primordia remained at approximately the same stages of development in all types of shoots (table 1, stem tip 5). In a stem tip of Hale peach from Southern California which had ceased to elongate there were just a few isolated fibers which were completely lignified in the median trace from the thirteenth leaf. The walls of other fiber initials were just beginning to lignify and secondary sieve tubes were present.

**Anatomy of the Peach Stem Undergoing Secondary Growth.** A peach stem in the early stages of secondary growth consists of the following tissues as observed in transverse sections. The outermost tissue of the stem is composed of a single layer of epidermal cells which has a thick cuticle. Inside this there are elliptical parenchyma cells which are arranged in periclinal rows, with their long axes oriented tangentially (fig. 19). This is the only type of cell in the cortex. Occasional cortical cells may contain calcium oxalate crystals which fill the cells and cause them to enlarge greatly, and in some instances to disintegrate (fig. 19). Large air spaces occur between the tangential rows of cortical cells. As the stem becomes less succulent, a periderm is formed. As De Bary (1884) reported, it is formed in the layer of cells immediately below the epidermis. Eames and McDaniels (1925) record a seasonal activity of a persistent cork cambium in *Prunus serotina*. This is also the case in peach. Next to the cortex occur the isolated groups of primary-phloem fibers. Inside these occur tangentially flattened parenchyma cells and sieve tubes of the primary phloem (fig. 19). As the stem increases



in circumference, the primary phloem bundles (consisting of primary-phloem fibers and inactive metaphloem) become separated. Increase in girth is accompanied by tangential elongation and division of the parenchyma cells between them (fig. 18). A ring of secondary phloem occurs between the primary phloem bundles and the cambium. It is divided into blocks by radially arranged vascular rays. The blocks of secondary phloem contain thin-walled parenchyma cells, thick-walled sieve tubes which have transverse or oblique sieve plates, and companion cells. Some phloem parenchyma cells may contain calcium oxalate crystals which cause the cell walls to distintegrate. De Bary (1884) noted similar cavities in *Prunus*. Centrally to the phloem lies the vascular cambium, then follows the xylem.

In stems two or more years old, secondary growth causes the previous year's phloem to be crushed against the primary-phloem fibers. Sometimes the phloem ray cells are also crushed, but more often they are bent by the increase in girth. Cells of ray portions several layers thick may be elongated tangentially and the girth of the obliterated phloem region thus increased. When this occurs the length of such rays in the crushed phloem region is decreased without bending of the rays. The primary-phloem fibers become isolated in tissue composed of tangentially elongated parenchyma cells formed from the folded vascular rays. Thin layers of flattened cells may be seen curving into this parenchymatous tissue, each of which represents a crushed block of secondary phloem. Because of the obliteration of the non-functioning phloem, the bark of peach trees remains relatively thin.

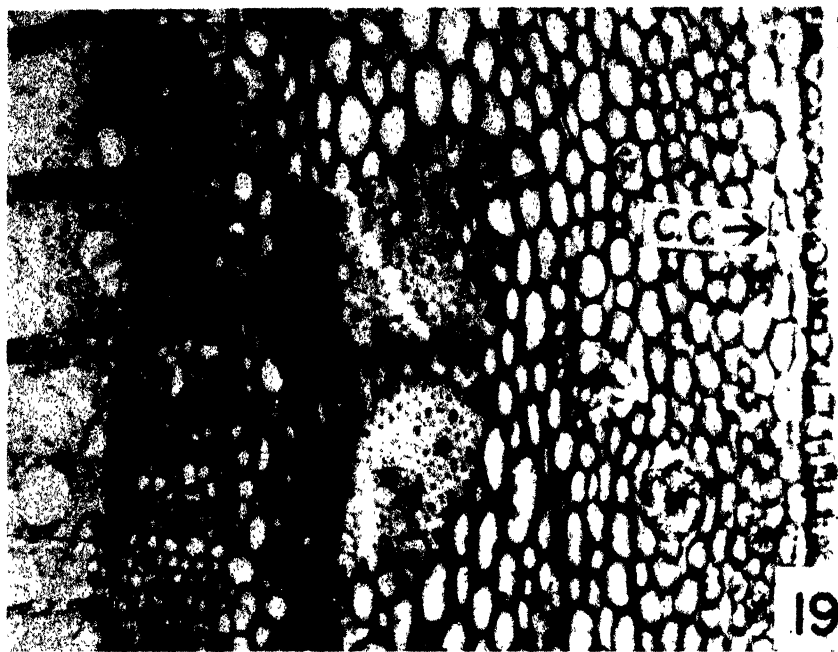
#### ANATOMY OF SWEET CHERRY BARK

Bastin (1895) made a study of the general features of bark several years old as it appeared in some of the cherries native to North America. The species considered were *P. serotina* Ehphart, *P. avium* L., *P. mahaleb* L., *P. pennsylvanica* L., and *P. virginiana* L. His terminology is difficult to understand and it seems desirable to redescribe the anatomy of the bark of *Prunus avium* from the point of view of ontogeny and seasonal changes.

Young sweet cherry stems in the process of secondary growth are very much like those of peach. The cells of the cortex are arranged in tangential rows with air spaces between the rows. Sclereids (which are absent in the peach) eventually ramify through the cortex. The development of these

#### Explanation of figures 17, 18

Transverse sections from peach stems. FIG. 17. 32 cm. from the stem tip and in the 6th fully elongated internode. Secondary phloem is just beginning to form.  $\times 230$ . FIG. 18. 85 cm. from the tip of the same stem. Most of the sieve tubes of the primary phloem have been obliterated. Sieve tubes of the secondary phloem have thick crenulated walls. Lumina of some of the sieve tubes in the secondary phloem appear closed because of the presence of sieve plates.  $\times 180$ . One primary phloem bundle is set off by a line in each photograph. Celloidin sections stained with safranin and Delafields haematoxylin.



variously branched and shaped cells from parenchyma like initials has been described by Bergmann (1913) in *Prunus*. Primary-phloem fibers differentiate in the outer portion of the primary phloem bundles, and metaphloem is eventually crushed centrally to these. Primary phloem bundles are separated at most levels in the stem from the secondary phloem and from each other by large parenchyma cells. The secondary phloem area may be easily distinguished from the primary phloem by the straight rows of ray cells which it contains. No mature fibers are present in the functioning secondary phloem. They mature each growing season in the non-functioning phloem of the previous year (fig. 21).

In stems more than one year old, the phloem of previous years is not completely crushed by the new growth as it was found to be in peach. The partially crushed phloem is composed of rays several cells wide between which are cavities, parenchyma cells and partially collapsed sieve tubes. Secondary phloem fibers differentiate between the rays of the non-functioning phloem. They are not in bundles as are the primary phloem fibers but intermingle with old conductive tissues (fig. 21). Occasional sclereids of the type found in the cortex are present. The rays in phloem several years old appear wavy in transection, and the longer ones terminate at the primary phloem fibers.

In the fall and winter the layer of phloem present contains sieve tubes and parenchyma cells which are smaller than those found in the summer. These sieve tubes were without definitive callus on the sieve plates on January 5, 1942 (fig. 20). Summer sieve tubes were partially collapsed and definitive callus was present on the sieve plates. Parenchyma cells located near the rays and containing calcium oxalate crystals deteriorate and thus cause the formation of the cavities between the rays and the phloem tissue. During the summer fibers mature in the phloem of the preceding season. They are more abundant in the phloem of the previous autumn and winter than in the previous year's summer phloem (fig. 21). Gill (1932) has found in ash (*Fraxinus excelsior* L.) that large summer sieve tubes and small autumn sieve tubes are produced. Elliott (1935) on the other had found in *Acer pseudoplatanus* L. that large spring sieve tubes differentiate from thin-walled cells present during the previous winter and that the sieve tubes produced continuously during the summer from renewed action of the cam-

#### Explanation of figures 19, 20

FIG. 19. Transverse section of the bark of peach (Hale variety). Some subepidermal cells have divided to initiate the cork cambium (c.e.). Calcium oxalate crystals have caused two cortical cells to enlarge and decompose. The primary phloem has been partially flattened against the primary phloem fibers. Sieve tube walls stained deeper than phloem parenchyma.  $\times 200$ . FIG. 20. Transverse section of Sweet Cherry stem. Collected Jan. 25, 1942, at Green Valley. Summer sieve tubes are partially collapsed and sieve plates are callused (arrows point to 2 callused sieve plates). Cavities have developed between the rays and the phloem area. Thick-walled cells near the cambium with no contents are winter sieve tubes (two of them have circles drawn in their lumina).  $\times 370$ .





bium are relatively smaller. In sweet cherry the callus disappears from the partially collapsed sieve tubes the summer following their cessation of activity.

The summer sieve tubes are very large and may be the dominant type of cells between the rays (figs. 21, 22). The middle lamella and the original primary walls of sieve tubes contain pectic substances and stain black with Heidenhain's haematoxylin. The nacré walls which are reported to be of almost pure cellulose (Esau 1939) stain red with congo red, a cellulose stain (Conn 1940) (fig. 22). Slit-shaped cavities have been observed in some preparations in the nacré walls, and they are arranged in a concentric manner around the entire cell wall. In a longitudinal section of a sieve tube which was stained for cellulose with IKI and sulfuric acid (Rawlins 1933), the middle lamella and callus dissolved away, the cell walls were blue, and the protoplasmic connections turned yellow (fig. 24). Protoplasmic connections in some sieve plates appeared to be tubular when observed in transverse section (fig. 23). The material for sections in which this phenomenon was observed was collected in July at Green Valley and was fixed in alcohol-formalin-acetic no. 1 (Rawlins 1933), sectioned 2 microns thick in paraffin, stained by the azure II and basic fuchsin method, and mounted in glycerol. In material prepared in this manner (fig. 23) the black area between the protoplasmic connections is the cell wall, white rings are callus and the black rings inside the white rings are presumably protoplasm. In longitudinal view, protoplasmic connections also appear tubular (fig. 25). Connections also appear tubular after the same material is stained with safranin and gentian violet, eosin, or Heidenhain's haematoxylin. The tubular nature of the connections was only apparent in the large summer sieve tubes of vigorously growing orchard trees.

The nature of the connections between sieve tube elements still appears obscure. Some workers describe these connections as protoplasmic tubules enclosing vacuolar material (see review by Esau, 1939). Crafts (1932, 1933, 1939a, 1939b) and some other workers, however, doubted that the connections between sieve-tube elements are tubular and interpret them as solid protoplasmic strands. It is suggested here that slime which ordinarily coagulates on sieve plates during the process of removing and fixing stems for sectioning may plug the tubular connections and cause them to appear solid. Crafts (1933) and others have shown that sieve tube slime is suspended in

#### Explanation of figure 21

Transverse section of Sweet Cherry stem. Collected in July 1941. There is a wide band of functioning summer phloem next to the cambium. Large cells between the rays are sieve tubes and small cells are phloem parenchyma and companion cells. On the outside of the functioning phloem part of the obliterated phloem of previous years is shown. Sieve tubes and some of the parenchyma cells are partially or completely crushed. Fissures occur along the rays. The arrow points to fibers which have appeared in the degenerating tissues.  $\times 88$ .



Sections of Sweet Cherry sieve tubes. Collected in July 1941. FIG. 22. Transverse section stained with Heidenhain's haematoxylin and Congo red. Mounted in glycerol. The original cambial walls and middle lamella stained black and the nacré walls stained red.  $\times 575$ . FIG. 23. Sieve plate in face view and free of slime. Stained with azure II and basic fuchsin; mounted in glycerol; cut  $2\mu$  thick. Cell walls and cytoplasm are black, callus rings are white.  $\times 1500$ . FIG. 24. Longitudinal section of sieve tube at a sieve plate. Treated with IKI and mounted in 50 per cent sulfuric acid. The pectic middle lamella and the callus have dissolved. Protoplasmic connections are present. Slime is present on one side of the sieve plate and also fills the protoplasmic connections.  $\times 1130$ . FIG. 25. Longitudinal sections of a sieve tube at a sieve plate. Stained with azure II and basic fuchsin and mounted in glycerol; sectioned  $4\mu$  thick. Original cambium walls and cytoplasm are black. Callus, middle lamella, and nacré walls are white. Position of the vacuolar connections are shown by arrows.  $\times 1125$ .

the vacuoles of the elements. When a segment of a stem is removed, sieve tube contents move from the center of the segment toward each end and are coagulated by ordinary fixatives on the side of the sieve plates away from the cut

surface. The sieve plates in the center of the stem segment remain free of slime since the contents of adjoining elements move in opposite directions (Crafts 1939a, fig. 5). Sieve plates of figures 23 and 25 are free of slime and consequently the connecting strands appear tubular. Figure 24 shows slime accumulated against one side of a sieve plate and here the strands appear solid.

#### SUMMARY

The development of the primary and secondary phloem of peach and the secondary phloem of cherry have been studied.

In the peach the first protophloem sieve tube was found in the fifth or sixth leaf primordium. The first sieve tube develops in the center of the abaxial side of the median leaf trace. Subsequent ones develop laterally and adaxially to the first. As seen in transverse section of a young leaf trace, the procambium is a layer of polygonal cells between the primary xylem and primary phloem which usually divide more nearly in a periclinal than an anticlinal direction. Certain cells initiated by the procambium differentiate into primary ray cells which divide the primary phloem into strands. As obliteration of protophloem sieve tubes occurs, the outer cells of the protophloem elongate, lay down secondary walls, and become lignified, thus forming the primary-phloem fibers. Elongation of similar cells without formation of secondary walls or lignification occurs in the petioles and leaves. There is a lag between the time at which the last metaphloem mother cells are initiated and that when the production of secondary phloem in the stems begins. During this lag, the last cells to be initiated on the phloem side by the procambium enlarge to form large parenchyma cells which separate the secondary phloem from the primary phloem, and metaphloem sieve tubes slowly develop from initials previously laid down. The procambium is then transformed into the cambium which initiates only xylem during the period in which the metaphloem sieve tubes differentiate from the mother cells previously laid down.

As the stem increases in girth by cambial activity, the strands of primary phloem fibers become removed from each other; they eventually appear on the periphery of the secondary phloem as isolated groups of fibers with crushed metaphloem on their inner sides.

For a time following maturation, secondary sieve tubes have thick nacre walls which nearly fill the lumina of the sieve tubes.

Secondary phloem of previous years is quite completely crushed and obliterated by newly produced phloem in peach. Hence the bark of peach remains thin.

In sweet cherry the new band of secondary phloem produced each spring functions during the summer and autumn. In late autumn the sieve tubes partially collapse and definitive callus forms on the sieve plates. A few small

sieve tubes near the cambium maintain their turgidity throughout the winter. During each growing season secondary phloem fibers mature in the phloem formed in the previous summer. Fissures occur along the rays in this old phloem tissue. Little crushing of old secondary phloem occurs in cherry and therefore the bark of cherry is thicker than that of peach.

Protoplasmic connections through the pores of sieve plates of sweet cherry are very large and appear to be tubular in sieve plates free of slime.

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**FURTHER STUDIES ON THE ANTIBIOTIC  
ACTIVITY OF LICHENS\***

PAUL R. BURKHOLDER AND ALEXANDER W. EVANS

The production by bacteria, molds, algae, and flowering plants of antibiotic substances inimical to the life processes of other organisms has been clearly demonstrated with simple laboratory techniques by which small amounts of the active materials are supplied to assay microorganisms cultivated under suitable conditions. In an earlier report from our laboratory it was shown that lichens also possess antibacterial properties (1). Continuation of these studies has led to the accumulation of additional data concerning the antagonistic effects observed when approximately one hundred kinds of lichens were tested against selected species of bacteria including some pathogenic strains. We present herewith a summary report together with a brief discussion concerning the possible significance of the observations.

**METHODS**

The lichens were collected principally in Connecticut, in the Cape Cod region of Massachusetts, and in the White Mountains of New Hampshire. Some specimens were gathered for this work also by Dr. A. J. Riker in Wisconsin, and by Mr. C. A. Weatherby while on vacation in New Brunswick. Specimens from the Alcan Highway were supplied by Dr. H. M. Raup. Dr. Werner Bergmann also made available some interesting materials from the Sterling Laboratory of Chemistry of Yale University. The lichens were placed in shallow pans in the laboratory, moistened periodically with water, and exposed to daylight for the purpose of keeping them physiologically active. It should be mentioned, however, that a few of our later tests on dried specimens indicate that the active materials, in some lichens at least, are stable during storage for many years. Extracts were prepared by grinding with a glass mortar and pestle 100 mg. of lichen in 1 ml. of phosphate buffer solution adjusted to pH 7.4. The buffer solution was made by mixing 80.8 ml. of M/15  $\text{Na}_2\text{HPO}_4$  and 19.2 ml. of M/15  $\text{KH}_2\text{PO}_4$ . The reaction of the aqueous suspensions of lichen materials was measured with color indicator papers before making the tests, and when necessary the pH was adjusted with dilute alkali to 7.0.

The assay procedure involved the use of the cylinder plate method of testing antibiotic potency of the extracts against bacteria in Petri-dish cultures (2). Agar plate suspensions of the test bacteria were prepared in the

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usual way and, after gelation of the medium was complete, small glass cylinders were arranged on the surface of the agar as indicated in figures 1 and 2. Difco yeast-beef-dextrose agar was employed as the nutrient medium, and the cups were "penicillometers" purchased from the Fisher Scientific Company. With a free-flowing pipette, 0.2 ml. of each lichen preparation was transferred to a cup. After a period of incubation, usually 15 hours at 37° C, zones of bacterial growth-inhibition subjacent to the cylinders were taken as an indication of antibacterial potency.

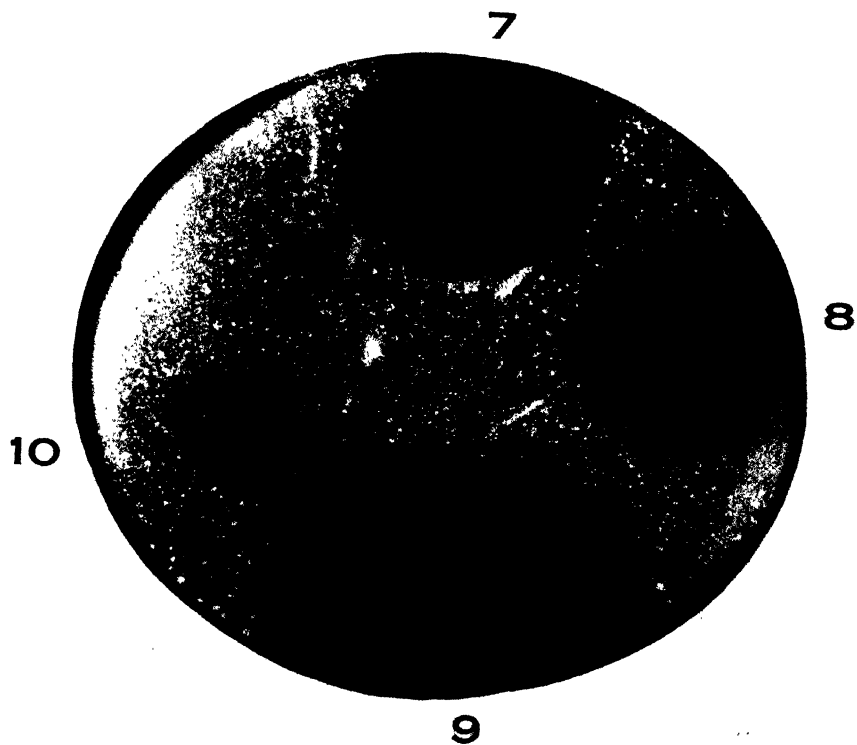
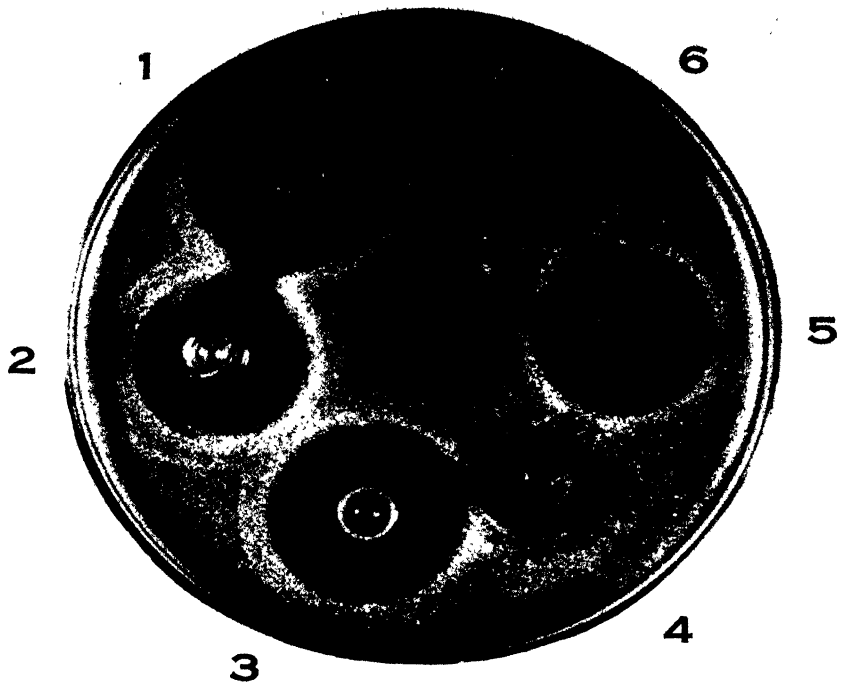
An attempt was made to test each of the collected lichens against *Staphylococcus aureus*, *Bacillus subtilis*, and *Escherichia coli*. In addition to these, certain other bacteria which were used in testing some of the lichens are the following: *Acrobacter aerogenes*, *Alcaligenes fecalis*, *Proteus vulgaris*, *Serratia marcescens*, *Bacillus cereus*, *B. mycoides*, *Clostridium Welchii*, *Diplococcus pneumoniae*, *Lactobacillus casei*, *Sarcina lutea*, *Staphylococcus albus*, *Streptococcus hemolyticus*, and *S. viridans*. Some of these organisms were supplied by Prof. S. A. Waksman, Rutgers University, and others were obtained through the kindness of Prof. P. B. Cowles, Yale University School of Medicine.

#### OBSERVATIONS

The results of our tests with different lichen extracts show varying degrees of activity ranging from strong growth promotion to marked inhibition. Some characteristic inhibition zones which were obtained with *B. subtilis* and *S. lutea* are illustrated in figure 1. Concentric patterns of growth promotion lying outside the region of inhibition, as in the plate of *B. subtilis* shown in the upper part of the figure, are found frequently in these tests and are the object of discussion in another paper (3). Tests with the sensitive *S. lutea* yield comparatively large zones of inhibition, as is shown in the lower part of figure 1. During the relatively long incubation period of about 36 hours necessitated by the slow growth of this organism, there is sufficient time for diffusion of an antibacterial substance to a considerable distance from the cup. The extent to which diffusion of the antibiotic substance takes place prior to growth of the test bacteria determines largely the diameter of the zone of inhibition. Both *Bacillus subtilis* and *Sarcina lutea* are excellent test organisms for use in teaching-demonstrations of antibiosis, provided smooth suspensions of the bacteria are employed in making the pour plates. Relative stability of at least some of the antibiotic lichen compounds is indi-

#### Explanation of figure 1

Antibacterial action of lichen extracts at pH 7.0 in cups, tested against bacteria in yeast-beef-dextrose agar. Above, *B. subtilis* grown for 16 hours at 37° C; 1, *Cladonia pleurota*; 2, *C. mitis*; 3, *C. uncialis*; 4, *Stereocaulon paschale*; 5, *Parmelia euperata*; 6, *Cladonia sylvatica*. Below, *S. lutea* grown for 36 hours at 25° C; 7, *Cladonia Grayi*; 8, *C. sylvatica*; 9, *C. cristatella*; 10, *C. rangiferina*.



cated by the fact that the tests with *Sarcina lutea* shown in figure 1 were made with lichen materials which had been allowed to dry in the laboratory for several months. The activity of several species of lichens was not lost by boiling in  $\text{Na}_2\text{CO}_3$  solution for several minutes, which indicates that we are dealing with substances very different from penicillin.

It has been found generally that samples of a species of lichen collected from different regions show characteristic activity in antibiotic tests with suitable bacteria. Occasionally, however, some samples of a species which hitherto has given indications of activity fail to inhibit bacterial growth. No satisfactory explanation for this variability is known, although it may be of significance to point out that some of the diagnostic acids have been reported to occur in varying amounts in different samples of some species of lichens.

Thirty-five species of *Cladonia* have been found active against either *B. subtilis* or *S. aureus* or against both of these bacteria. Species observed to be active against both test bacteria are the following: *C. borbonica*, *C. caespiticia*, *C. capitata*, *C. cristatella*, *C. glauca*, *C. Grayi*, *C. merochlorophaea*, *C. nemoxya*, *C. papillaria*, *C. pyxidata* (variable against *B. subtilis*), *C. squamosa*, and *C. strepsilis* (somewhat variable for *B. subtilis*, see figure 2, no. 4). Species inhibiting *B. subtilis* but not *S. aureus* are: *C. amaurocraea*, *C. alpestris*, *C. atlantica*, *C. bacillaris*, *C. Boryi*, *C. brevis*, *C. caroliniana*, *C. coniocraea*, *C. cyanipes*, *C. deformis*, *C. fimbriata*, *C. gracilis* var. *chordalis*, *C. incrassata*, *C. macilenta*, *C. mitis*, *C. pityrea*, *C. pleurota*, *C. Robbinsii*, *C. submitis*, *C. subtenuis*, *C. sylvatica*, *C. uncialis*. Species which were active against *S. aureus* but not inhibitory for *B. subtilis* are *C. cryptochlorophaea* and *C. gonecha*.

The occurrence of various characteristic acids in these species of *Cladonia* has been considered from the standpoint of a possible explanation for the observed antibacterial activities. The published work of several investigators provides information in this field (4, 5, 6, 7). In the group of 35 active species of *Cladonia*, characteristic compounds are found with varying frequency in the different kinds of lichens. Usnic acid occurs in 17 of the species, fumarprotocetraric acid in 14, squamatic acid in 7, substance A in 6, substance F in 6, barbatic acid in 6, didymic acid in 4, substance B in 3, substance C in 2, substance E in 2, baeomyelic acid in 2, psoromic acid in 2, Zeorine in 2, bellidiflorine in 2, grayanic acid in 2, and substance D, substance G, strepsiline, cryptochlorophaeic acid, perlatolic acid, merochlorophaeic acid, homosekikaic acid, thamnolic acid, and atranorine each in one but not the same species. Although we have only meagre evidence for the theory that antibiosis in lichens is related to the constituent diagnostic compounds, still the structural similarity between known inhibitory substances and certain lichen acids is highly suggestive. The possible use of this type of information will be illustrated with one example.

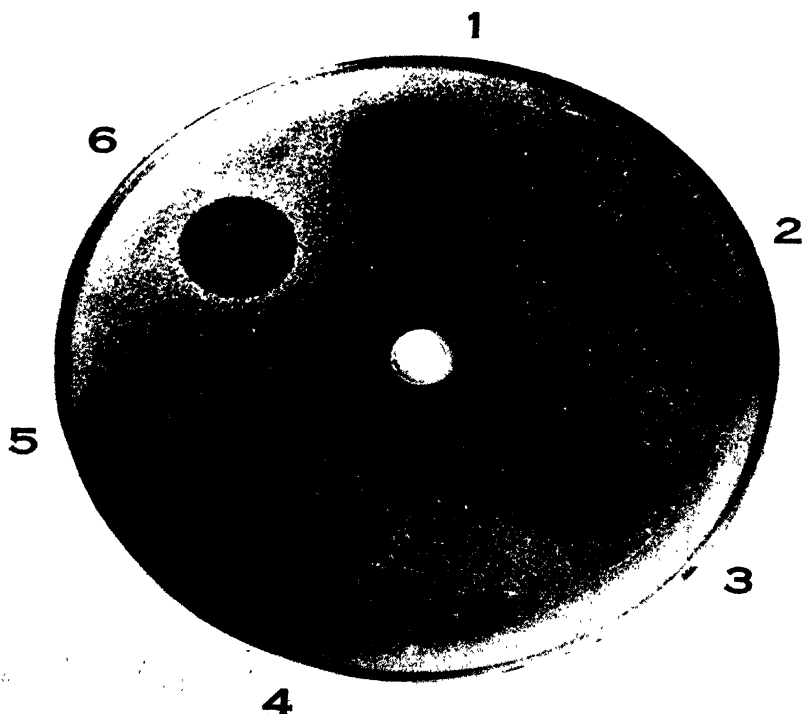
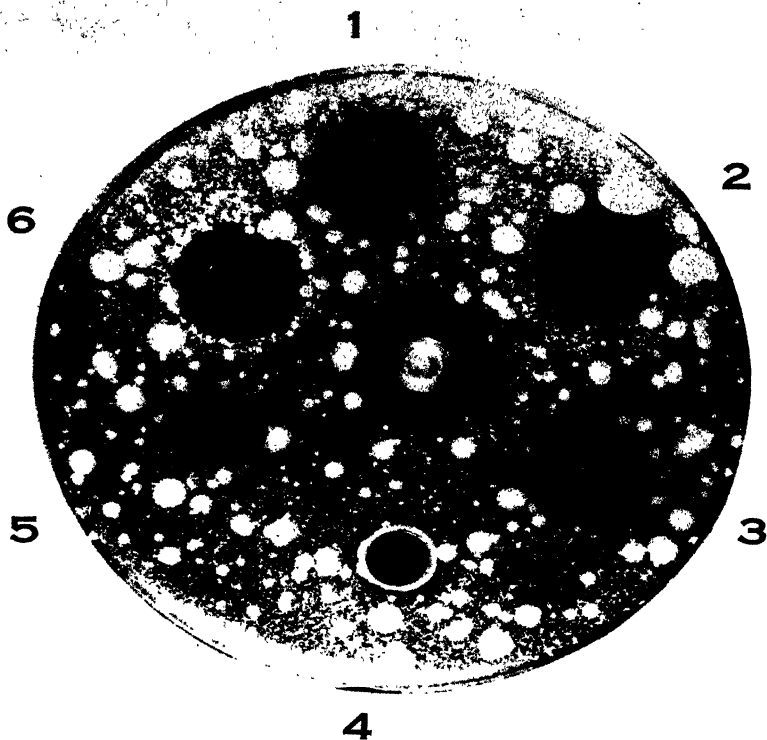


Three typical lichen compounds, atranorine, fumarprotocetraric acid, and usnic acid, were obtained from vials accompanying herbarium specimens of Sandstede's *Cladonia exsiccatae* in Yale University. Cylinder plate tests indicated that usnic acid is active against *B. subtilis* but not against *S. aureus* or *E. coli*. Usnic acid, crystallized from a species of *Usnea* and supplied to us by Prof. Werner Bergmann, likewise showed activity in tests with *B. subtilis*. Usnic acid is practically insoluble in water, and for this reason a saturated solution with a few minute crystals in excess was employed in making the tests (see figure 2). Atranorine and fumarprotocetraric acid were inactive against the three bacteria used in these tests.

TABLE 1. Comparative antibiotic activity of extracts from 11 species of lichens tested against 13 kinds of bacteria. Diameter of inhibition zone is given in mm. Diameter of cup is 8 mm.

Species of bacteria	Species of lichens										
	<i>Usnea florida</i>	<i>Stereocaulon paschale</i>	<i>Parmelia physodes</i>	<i>Parmelia caperata</i>	<i>Cladonia uncialis</i>	<i>Cladonia sylvatica</i>	<i>Cladonia pleurota</i>	<i>Cladonia mitis</i>	<i>Cladonia cristatella</i>	<i>Cetraria nivalis</i>	<i>Cetraria cucullata</i>
<i>Staphylococcus aureus</i>	0	17	10	13	0	0	0	0	0	0	0
<i>Staphylococcus albus</i> (hemolytic)	0	0	11	0	12	10	13	12	9	0	12
<i>Diplococcus pneumoniae</i>	0	0	0	11	12	12	15	14	9	0	12
<i>Streptococcus hemolyticus</i>	0	0	0	12	10	0	10	10	0	0	10
<i>Streptococcus viridans</i>	0	0	0	15	9	0	12	11	0	0	11
<i>Bacillus subtilis</i>	17	20	10	24	26	26	29	24	21	15	22
<i>Bacillus mycoides</i>	16	12	0	17	19	19	20	20	16	17	21
<i>Sarcina lutea</i>	30	13	12	25	25	34	32	28	38	40	36
<i>Serratia marcescens</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Proteus vulgaris</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Alcaligenes fecalis</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Aerobacter aerogenes</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Escherichia coli</i>	0	0	0	0	0	0	0	0	0	0	0

Diagnostic compounds known to occur in the antibiotic species of *Cladonia* have been listed but other unidentified substances might be responsible for the observed antibacterial properties. Many species which do not contain usnic acid are capable of inhibiting *B. subtilis*, and this acid does not explain the inhibition of *S. aureus* by many lichens. Although completely unknown substances remain to be discovered in these primitive plants, still it seems probable that the preparation of a series of characteristic compounds from antibiotic lichens might provide a means of identifying the substances which are the basis for chemical antagonisms observed in our survey. Following the clear demonstration of antibacterial activity exhibited by lichen sub-



stances of known chemical structure, there would remain for the organic chemist the attractive possibility of preparing derivatives with selective activity against different kinds of protoplasm. Investigations in this field have been initiated in the Yale laboratories.

The species of lichens for which activity against *B. subtilis* is illustrated in figure 1 were tested along with other lichens against additional species of bacteria. Typical data are presented in table 1. In this group of lichens no activity was found against the five kinds of Gram-negative bacteria listed. All of these lichens were active against *B. subtilis* and *Sarcina lutea*. In a few tests made with the anaerobe *Clostridium Welchii*, extracts of *Cladonia mitis* and *C. pleurota* were found inhibitory. *Lactobacillus casei* was strongly inhibited by several of the species of *Cladonia* which were active against *B. subtilis*. Comparatively small zones of inhibition were observed for the Gram-positive pathogenic bacteria.

When tested against Gram-negative bacteria, most lichens appear to have little or no antibiotic activity. In a few tests made with the Gram-negative *Alcaligenes fecalis*, the following lichens exhibited some activity: *Cladonia delicata*, *C. glauca*, *Parmelia conspersa*, *P. rudecta*, *Thamnolia vermicularis*, and *Xanthoria parietina*. Active against *E. coli* were *C. borbonica* and *P. rudecta*, and against *Proteus vulgaris* the lichens *Parmelia physodes* and *Umbilicaria papulosa* showed slight inhibition.

In addition to the lichens already listed in table 1 or mentioned in the discussion, other species which were found to be antibiotic for either *S. aureus* or *B. subtilis* or for both of these bacteria are the following: *Alectoria chalybeiformis* (variable against *B. subtilis*), *Bacomyces aeruginosa*, *Cetraria juniperina*, *C. Oakesiana*, *Dactylina arctica*, *Dermatocarpon miniatum*, *Evernia vulpina*, *Lepra* sp., *Nephromopsis ciliaris*, *Parmelia conspersa*, *P. rudecta*, *Physcia* sp., *Ramalina* sp., *Rhizocarpon* sp., *Sphaerophorus globosus*, *Thamnolia vermicularis*, *Umbilicaria papulosa*, and various species of *Usnea*. The sample of *Evernia vulpina*, contributed by Dr. Werner Bergmann, came from material which had been stored for a number of years in the Department of Chemistry at Yale University.

Species of lichens which were found inactive when tested against *S. aureus* and *B. subtilis* are the following: *Bacomyces placophyllus*, *B. roseus*, *Cetraria islandica*, *Cladonia apodocarpa*, *C. chlorophaea*, *C. clavulifera*, *C. conista*, *C. delicata*, *C. furcata*, *C. gracilis* var. *dilatata*, *C. gracilis* var. *elongata*, *C. mateocynthia*, *C. ochrochlora*, *C. rangiferina*, *C. santensis*, *C. scabriuscula*, *C. squamosa* var. *denticollis*, *C. subcariosa*, *C. turgida*, *C. verticillata*, *Lobaria pulmonaria*, *Parmelia Cladonia*, *Peltigera variolosa*, *Umbilicaria*

#### Explanation of figure 2

Antibacterial action of usnic acid and extracts from six species of lichens. Above, *S. aureus*; below, *B. subtilis*. The cup in the center of each plate contained usnic acid. Peripheral cups contained extracts from the following lichens: 1, *Cladonia caccapitica*; 2, *C. cristatella*; 3, *Parmelia physodes*; 4, *C. strepsilis*; 5, *C. capitata*; 6, *C. Grayi*.

*Dillenii*, and *Xanthoria parietina*. Several unidentified specimens belonging in the genera *Cetraria* and *Parmelia* were also inactive. It is possible that other specimens of these lichens might be found active against these or other test organisms. As an example, many samples of *Cladonia rangiferina* were observed to be inactive against *B. subtilis* and *S. aureus*, but when tested against *Sarcina lutea* some antibiotic activity was shown (see figure 1).

Our observations indicate the presence of antibacterial substances in numerous species of *Cladonia* and in representatives of other genera of lichens. Among these primitive plants, chemical antagonism appears to be a defense mechanism against Gram-positive airborne bacteria. Whether the active agents are to be regarded as bactericidal or merely bacteristatic is not proved. Transfers of agar suspensions from the inhibition zones of *S. aureus* test organisms which had been treated with extracts from *Cladonia cristatella*, *C. cryptochlorophaea*, *C. Grayi*, *C. coniocraea*, and *Parmelia physodes* grew well in fresh nutrient agar. Transfers of *B. subtilis* which had been inhibited by similar extracts failed to grow in nutrient agar or broth. It may be that the inhibitory substances produced by lichens prevent temporarily the growth of some microorganisms and actually kill others. The phenomenon of antibiosis, which seems to be widespread in nature and of great significance as a factor in ecology, is well exemplified in the lichens.

#### SUMMARY

Of the approximately one hundred kinds of lichens tested for antibiotic activity against bacteria, fifty-two were found to inhibit either *Bacillus subtilis* or *Staphylococcus aureus* or both of these species. Although Gram-positive bacteria including several pathogenic types are inhibited, Gram-negative bacteria with a few exceptions are generally not susceptible to the antibiotic substances of lichens. Usnic acid, obtained from *Cladonia mitis* and *Usnea florida*, inhibited *B. subtilis*. The significance of other characteristic compounds known to be present in lichens is discussed in relation to their possible antibacterial activity.

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## A SURVEY OF SOME WOOD-DESTROYING AND OTHER FUNGI FOR ANTIBACTERIAL ACTIVITY<sup>1</sup>

WILLIAM J. ROBBINS, ANNETTE HERVEY, ROSS W. DAVIDSON,  
ROBERTA MA AND WILLIAM C. ROBBINS

Fleming's discovery (1) of the production of penicillin by *Penicillium notatum*, and its development as an important therapeutic agent, have stimulated new interest in the antibiotic activity of the fungi. Reviews of earlier work have been published by Waksman (4, 5), Porter and Carter (2), and Weindling (6). Wilkins and Harris (7) have reported on the production of bacteriostatic substances by about 100 fungi belonging mainly to the genera *Penicillium* and *Aspergillus*. This paper presents a survey of the antibacterial activity of over 300 wood-destroying fungi, 22 dermatophytes, and about 50 miscellaneous fungi against *Staphylococcus aureus* and *Escherichia coli*. The antibiotic effects for any fungus are influenced by a number of factors, including the strain of the fungus, the medium used for its cultivation, the length of the growth period, the organism used in assay, and the method of assay. The results in this paper should not be considered as absolute, but preliminary and suggestive for later and more detailed investigation.

**Preliminary Experiments, Miscellaneous Fungi.** In some preliminary experiments<sup>2</sup> a modification of Fleming's streak method of assay (1) was used for testing the antibacterial activity of a group of miscellaneous fungi. The fungus to be tested was inoculated at the side of a Petri dish, 15 × 100 mm., containing 15 ml. of an agar medium and grown at 25° C until it had reached a diameter of 2 or 3 cm. or, if it grew slowly, until it was a week or more old. The bacteria (a broth culture from 1 to 10 days old) were then streaked up to the edge of the fungus colony. *Staphylococcus aureus* and *Escherichia coli* were used as test organisms because they represented gram-positive and gram-negative organisms respectively. The streaked plates were incubated overnight at 37 ± 2° C and inspected for the absence of bacterial growth adjacent to the fungus colony.

The medium on which the fungi were grown contained per liter 10 g. dextrose, 1.5 g. KH<sub>2</sub>PO<sub>4</sub>, 0.5 g. MgSO<sub>4</sub> · 7H<sub>2</sub>O, 1 g. neopeptone, 1000 mμ moles thiamine, and 20.0 g. of Difco agar.<sup>3</sup> It was adjusted to neutrality with NaOH.

<sup>1</sup> This investigation was supported in part by contributions from members of the Garden Club of America and of the Garden Club of Englewood, N. J. Publication costs were partially met by a gift from Mrs. Roy S. Hunt.

<sup>2</sup> These experiments were performed in June, 1943.

<sup>3</sup> Mineral supplements in p.p.m. were added as follows: 0.005 B, 0.02 Cu, 0.10 Fe, 0.01 Ga, 0.01 Mn, 0.01 Mo, and 0.09 Zn.

**Results with Streak Method for Miscellaneous Fungi.** No inhibition or doubtful results were obtained with the following fungi:

<i>Absidia orchidis</i> (+ and -)	<i>Fusarium avenaceum</i> (5 strains)
<i>Absidia ramosa</i> (+ and -)	<i>Gibberella saubinetii</i>
<i>Ashbya gossypii</i>	<i>Gibberella zeae</i> (2 isolations)
<i>Cephalosporium acremonium</i>	<i>Grossmannia serpens</i> (2 isolations)
<i>Ceratostomella ips</i> (2 isolations)	<i>Mucor mucedo</i>
<i>Ceratostomella fimbriata</i>	<i>Mucor ramannianus</i>
<i>Ceratostomella</i> from London plane tree	<i>Neurospora crassa</i>
<i>Ceratostomella microspora</i>	<i>Neurospora sitophila</i>
<i>Ceratostomella minutum</i>	<i>Ophiobolus oryzae</i>
<i>Ceratostomella montium</i>	<i>Ophiostoma catonianum</i>
<i>Ceratostomella multiannulata</i>	<i>Pholiota adiposa</i>
<i>Ceratostomella obscura</i>	<i>Phycomyces blakesleeanae</i> (+)
<i>Ceratostomella paradoxa</i> (3 isolations)	<i>Phytophthora cinnamomi</i>
<i>Ceratostomella penicillata</i>	<i>Polyporus versicolor</i>
<i>Ceratostomella piceaperda</i>	<i>Pythiomyces gonapodyides</i>
<i>Ceratostomella pilifera</i>	<i>Pythium butleri</i>
<i>Ceratostomella pini</i> (2 isolations)	<i>Pythium helicoideis</i>
<i>Ceratostomella pseudotsugae</i>	<i>Rhizopus nigricans</i> (+ and -)
<i>Ceratostomella radicleola</i>	<i>Schizophyllum commune</i>
<i>Ceratostomella stenoceras</i>	<i>Sclerotinia</i> from eggplant
<i>Chalaropsis thielavioides</i> (3 isolations)	<i>Sclerotinia</i> from opuntia
<i>Claviceps purpurea</i>	<i>Sporotrichum globulatum</i>
<i>Endoconidiophora adiposa</i>	<i>Trichophyton gypseum</i>
<i>Endoconidiophora coerulescens</i> (2 isolations)	

*Aspergillus niger*, *Ceratostomella rostricylindrica*, *C. ulmi*, *Sclerotium delphinii*, *S. rolsfii*, and *Stereum murrayi* produced antibiotic substances which inhibited the growth of *Staph. aureus* or *E. coli* for distances ranging from 3.0 to 15 mm. from the edge of the fungus colony. Three of these fungi (*Aspergillus niger* and the two species of *Sclerotinia*) produced considerable acid as judged by indicator paper, and it appeared probable that their antibiotic activity was to be accounted for by the lowering of the hydrogen-ion concentration in the vicinity of the fungus colony. *Stereum murrayi* and the two species of *Ceratostomella* had little effect on the reaction of the medium. Their antibiotic activity appeared to be caused by other substances than the hydrogen-ion.

#### **Antibiotic Activity of Wood-destroying Fungi and Dermatophytes.<sup>4</sup>**

Since three wood-inhabiting fungi included in the preliminary experiments evidenced antibiotic activity not accounted for by acid produced by the organisms, it seemed desirable to survey a considerable number of this group.

The extensive collection of wood-destroying fungi in the Division of Forest Pathology of the U. S. Department of Agriculture was made avail-

<sup>4</sup> Most of the fungi, except the dermatophytes, included in this portion of the survey are wood-destroyers. Some, however, for example *Morchella esculenta*, are not.

able to us. These are distinguished later in this paper by the stock numbers given with each fungus. Some of these numbers represent cultures from other workers in the United States and from the Department of Agriculture, Ottawa, Canada, which were received through exchange. Those marked (CBS) are from Centraal Bureau voor Schimmelcultures. In addition, Dr. Dow V. Baxter furnished us with some from his collection; these are marked by the letter (B). We included also a *Verticillium* and a *Volutella* from Dr. B. O. Dodge, and a group of 22 dermatophytes obtained from the American Type Culture collection (ATC), through the courtesy of the National Institute of Health (NIH), from Dr. R. Benham (RB), or isolated by ourselves.

**Survey of Wood-destroying Fungi by the Streak Method.** The procedure for surveying the antibiotic activity of the wood-destroying fungi and dermatophytes was similar to that used in the preliminary experiments described above. The fungi were grown at 25° C in Petri dishes, 15 × 100 mm., containing 15 ml. of 2 per cent malt agar or a thiamine-peptone agar.<sup>5</sup> At times ranging from 3 to 22 days after inoculation, depending on the rapidity with which the fungus grew, the plates were streaked with *Staph. aureus* and *E. coli* (a 24-hour broth culture) from the edge of the colony to the periphery of the dish, a procedure which was considered preferable to that used in the preliminary experiments. Outlining the fungus colony with wax pencil on the bottom of the dish fixed its limits at the time of streaking. The radius of the fungus colony was measured, and as a rule each fungus was tested at two different ages. *Staph. aureus* grew poorly on the 2 per cent malt. The agar in each plate of this medium was, therefore, coated with 10 ml. of a modified thiamine-peptone agar<sup>6</sup> before the streaking with bacteria. The plates were incubated for 24 hours at 37 ± 2° C and examined for evidence of inhibition of the growth of the bacteria. When inhibition was observed the distance from the edge of the fungus colony to the bacterial growth was measured.

**Results with Wood-destroying Fungi on Streak Plates.** One hundred and twenty-three of the fungi showed no inhibition of *Staph. aureus* or *E. coli* either on the thiamine-peptone medium or on the malt agar. These were as follows:

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<sup>5</sup> The malt agar was prepared by adding 2 per cent desiccated malt extract to 1.5 per cent Difco agar. The pH of this medium was 5.0–5.4. The thiamine-peptone agar contained per liter, 10 g. dextrose, 1.5 g.  $\text{KH}_2\text{PO}_4$ , 0.5 g.  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ , 1.0 g. neopeptone, 15 g. Difco agar, and 600 mμ moles of thiamine. The mineral supplements given earlier were also added. The pH of this medium was 5.5.

<sup>6</sup> This consisted of the thiamine-peptone agar plus 1000 mμ moles of nicotinamide per liter, and the  $\text{KH}_2\text{PO}_4$  replaced with a mixture of 1.069 g.  $\text{Na}_2\text{HPO}_4 \cdot 2\text{H}_2\text{O}$  and 0.545 g.  $\text{KH}_2\text{PO}_4$ . The pH of this medium was close to 7.0.

- Collybia velutipes* (55001)  
*Collybia radicata* (72084-R)  
*Coprinus radians* (S-249)  
*Corticium cremoricolor* (57082-R)  
*Corticium salmonicolor*  
*Cytidia salicina* (15184-Sp)  
*Daedalea ambigua* (57066-S)  
*Daedalea confragosa* (67939-S)  
*Daedalea unicolor* (72082 and 72153)  
*Eridia glandulosa* (72147-S)  
*Favolus canadensis* (52003)  
*Fomes calkinsii* (14667-S)  
*Fomes connatus* (71522-R)  
*Fomes densus* (52046-S)  
*Fomes everhartii* (57210-S and B)  
*Fomes fomentarius* (59010-S)  
*Fomes fraxineus* (50357-R)  
*Fomes igniarius* (86391)  
*Fomes igniarius* var. *laevigatus* (94020)  
*Fomes rimosus* (59124-S and CBS)  
*Fomes robustus* (71987-S)  
*Fomes robustus* var. *tsugina* (16836-S)  
*Fomes torulosus* (179)  
*Fomes* sp. (59163-R)  
*Hydnum chrysocomum* (1605)  
*Hydnum ochraceum* (71953)  
*Hydnum pulcherrimum* (50343-S)  
*Lentinus tigrinus* (50390-R)  
*Lentinus villosa* (57001)  
*Lenzites betulina* (13813-R)  
*Lenzites* sp. (1682)  
*Lenzites trabea* (539)  
*Merulius niveus* † (71734-R)  
*Merulius tremellosus* (94184)  
*Morchella esculenta*  
*Panus laevis* (71178-R)  
*Panus rudis* (1927)  
*Panus strigosus* (55699-S)  
*Peniophora allescheri* (56483-S)  
*Peniophora gigantea* (56475-S)  
*Peniophora pubera* (71412-R)  
*Pholiota adiposa* (59116-S)  
*Pholiota aurivella* (CBS)  
*Pholiota limonella* (71894-S)  
*Pholiota spectabilis* (72080)  
*Pleurotus corticatus* (75056-S)  
*Pleurotus ostreatus* (56478-S)  
*Pleurotus sapidus* (71958)  
*Pleurotus ulmarius* (71386-S)  
*Polyporus abietinus* (71429-R)  
*Polyporus adustus* (56476-S)  
*Polyporus anceps* (71825-S and 58526-R)  
*Polyporus arcularius* (30680)  
*Polyporus berkeleyi* (53379-S)  
*Polyporus brumalis* (56439-S)  
*Polyporus cinnabarinus* (57071-S)  
*Polyporus cuticularis* (71342-S)  
*Polyporus dichrous* (57474-S)  
*Polyporus distortus* (57059-S)  
*Polyporus dryadeus* (71092-S)  
*Polyporus dryophilus* (71539-R)  
*Polyporus ectypus* † (81034-R)  
*Polyporus fibrillosus* † (94071-R)  
*Polyporus flexilis* (50384-S)  
*Polyporus frondosus* (50222 and 72076-S)  
*Polyporus fumosus* (71335-S)  
*Polyporus gilvus* (56480-S)  
*Polyporus glomeratus* (71126)  
*Polyporus graveolens* (71021)  
*Polyporus hirsutus* (56479-S)  
*Polyporus hispidus* (59106-S and 43 Findlay)  
*Polyporus hydroides* (80938-R)  
*Polyporus leucoides* (50390-S)  
*Polyporus mutabilis* (57069-S)  
*Polyporus ossesus* (551)  
*Polyporus pargamensis* (57403-S)  
*Polyporus picipes* (59060-R)  
*Polyporus pinsitus* (71973-R)  
*Polyporus pubescens* (71448-R)  
*Polyporus robinophilus* (67904)  
*Polyporus resinosus* (B)  
*Polyporus rutilans* (2287)  
*Polyporus spumeus* (71929-S)  
*Polyporus spumeus* var. *malicola* (18565-S)  
*Polyporus squamosus* (CBS)  
*Polyporus subectypus* (57006)  
*Polyporus supinus* (57014-R)  
*Polyporus tenuis* (57012)  
*Polyporus tereanus* (94178-R)  
*Polyporus velutinus* (15067)  
*Polyporus versicolor* (71753-R)  
*Polyporus zonalis* (55571)  
*Polyporus zonatus* (CBS)  
*Poria ambigua* (86357)  
*Poria ferruginosa* (B)  
*Poria inermis* (B)  
*Poria nigrescens* (52041-S)  
*Poria obliqua* (58561-S and 59134-S)  
*Poria prunicola* (B)  
*Poria spiculosa* (94102)  
*Poria weirii* (B)  
*Ptychogaster cubensis* (300)  
*Schizophyllum commune* (56473-S)  
*Stereum albobadium* (71523-Sp)  
*Stereum hirsutum* (71556-Sp)  
*Stereum ochraceo-flavum* (123)  
*Stereum pini* (14780-R)  
*Stereum purpureum* (59171-R)  
*Stereum sanguinolentum* (1292-S)  
*Stereum spadiceum* (71427-Sp)  
*Trametes cubensis* (55613-S)  
*Trametes hispida* (68583-S)  
*Trametes rigida* (57004-R)  
*Trametes suaveolens* (71404-S)  
*Verticillium buxi* (D)  
*Volutella buxi* (D)



With the following fungi zones of inhibition of less than 5 mm. were observed on the thiamine-peptone agar for *Staph. aureus*:

<i>Armillaria mellea</i> (70973-R)	<i>Polyporus schweinitzii</i> (94095-R)
<i>Clitocybe tabescens</i> (512)	<i>Polyporus sulphureus</i> (71371-S)
<i>Corticium coerulescens</i> (14909)	<i>Polyporus varius</i> (2290)
<i>Corticium confluens</i> (71544-R)	<i>Poria ferruginosa</i> (B)
<i>Corticium galactinum</i> (72033)	<i>Poria inflata</i> (94089-S)
<i>Corticium roseum</i> (56489-S)	<i>Poria mutans</i> (72029-S)
<i>Fomes clandestini</i> (CBS)	<i>Poria prunicola</i> (94048-S)
<i>Fomes lobatus</i> (71656-R)	<i>Poria punctata</i> (50266-R)
<i>Hymenochaete curtisii</i> (71519-Sp)	<i>Stereum frustulosum</i> (24059)
<i>Lenzites trabea</i> (B)	<i>Stereum rameale</i> (86400)
<i>Lycoperdon gemmatum</i> (52001)	<i>Stereum roseo-carnum</i> (57416-S)
<i>Lycoperdon pyriforme</i> (64801)	<i>Stereum rufum</i> ?
<i>Pholiota lutea</i> (71389-S)	<i>Stereum sanguinolentum</i> (71776-R)
<i>Polyporus croceus</i> (47479-S)	<i>Stereum sericeum</i> (58500-R)
<i>Polyporus oregonensis</i> (1273)	

With the majority of this group the antibiotic activity was limited to *Staph. aureus* on the thiamine-peptone agar; there was none on malt agar, and none for *E. coli* on either kind of agar. *Polyporus varius* (2290) inhibited *E. coli* and *Staph. aureus* on the thiamine-peptone agar. *Corticium roseum* (56489-S), *Lycoperdon pyriforme* (64801), and *Stereum rameale* (86400) produced a slight zone of inhibition of *Staph. aureus* on both media. For *Daedalea unicolor* (72153) and *Lycoperdon gemmatum* (52001) a slight inhibition of *Staph. aureus* was observed on malt agar, but none on the thiamine-peptone medium.

The following 57 fungi produced zones of inhibition for *Staph. aureus* which ranged between 5 mm. and 10 mm. as a maximum:

<i>Clitocybe illudens</i> (72027-S)	<i>Peniophora cinerea</i> (57406-S)
<i>Clitocybe investiens</i> (56445-R)	<i>Peniophora coccineofulva</i> (57418-S)
<i>Echinodontium tinctorium</i> (80517-S)	<i>Peniophora incarnata</i> (56449-S)
<i>Fomes conchatus</i> (1403)	<i>Peniophora nuda</i> (56494-S)
<i>Fomes extensus</i> (CBS)	<i>Pholiota spectabilis</i> (71463)
<i>Fomes fulvus</i> (16870-S and CBS)	<i>Polyporus borealis</i> (91430)
<i>Fomes grottopis</i> (55521-S)	<i>Polyporus circinatus</i> (72026-a and 72026-S)
<i>Fomes igniarius</i> var. <i>populinus</i> (59024-S and A8)	<i>Polyporus compactus</i> (71339-S)
<i>Fomes marmoratus</i> (50332-S)	<i>Polyporus cristatus</i> ? (71774-S)
<i>Fomes pomaceus</i> (2283)	<i>Polyporus curtisii</i> (57051-S)
<i>Fomes rimosus</i> (53383-S)	<i>Polyporus dryophilus</i> var. <i>vulpinus</i> (71123)
<i>Fomes scutellatus</i> (1952-S)	<i>Polyporus ludovicianus</i> (55537-S)
<i>Hydnum coralloides</i> (59062-S and CBS)	<i>Polyporus pargamensis</i> (71954-S)
<i>Hydnum ericaceus</i> (55195-S)	<i>Polyporus schweinitzii</i> (86353)
<i>Hymenochaete agglutinans</i> (71707-R)	<i>Polyporus spraguei</i> (72025-S)
<i>Hymenochaete rubiginosa</i> (1650)	<i>Polyporus tuberaster</i> (2345)
<i>Lentinus lepideus</i> (F-1334)	<i>Polyporus tuckahoe</i> ( <i>tuberaster</i> ?) (72176)
<i>Lenzites saepiaria</i> (1-31-36)	<i>Polyporus volvatus</i> (14606)
<i>Lenzites trabea</i> (B)	<i>Poria andersonii</i> (72121-S)
<i>Merulius confluens</i> (15006-R)	<i>Poria carbonica</i> (8444)
	<i>Poria ferruginosa</i> (71181)

*Poria inflata* (72160-R)  
*Poria obliqua* (58567-S)  
*Poria undata* (P-151)  
*Poria unita* † (71598)  
*Poria* sp. (142)  
*Stereum frustulosum* (57048)

*Stereum gausapatum* (58555-S)  
*Stereum rameale* (57046)  
*Stereum rugosiusculum* (71516-Sp)  
*Stereum subpileatum* (58597-R)  
*Stereum sulcatum* (71690-R)  
*Stereum umbrinum* (52060)

With the majority of this group antibiotic activity was limited to *Staph. aureus* and usually on the thiamine-peptone agar and not on malt. Seventeen were observed to inhibit *E. coli* on the thiamine-peptone medium though in almost all instances the zone of inhibition was less than for *Staph. aureus*. These were *Clitocybe illudens* (72027-S), *Fomes fulvus* (16870-S and CBS), *F. pomaceus* (2283), *Hydnum coralloides* (59062-S and CBS), *H. erinaceus* (55195-S), *Lentinus lepideus* (F-1334), *Lenzites saepiaria* (1-31-36), *L. trabea* (B), *Peniophora cinerea* (57406-S), *P. incarnata* (56449-S), *Polyporus schweinitzii* (pine) (86353), *P. spraguei* (72025-S), *Poria carbonica* (8444), *P.* sp. (142), and *Stereum subpileatum* (58597-R).

One hundred and nineteen of the 332 fungi were observed to produce zones of inhibition for *Staph. aureus* of more than 10 mm. on one or both of the media used in the survey. The results are tabulated in table 1. The age in days of the fungus colony when the antibiotic activity was tested is given in column 2; the radius of the fungus colony on malt-agar in column 3; the inhibition zone measured from the edge of the fungus colony for *Staph. aureus* and *E. coli* in columns 4 and 5; the radius of the fungus colony on thiamine-peptone agar and the inhibition zones on that medium in columns 6, 7, and 8. An "A" shows those instances where we believe the acid produced by the fungus was considerable and the inhibition was caused by hydrogen-ion concentration. In all the experiments with the streak method of investigating the antibacterial activity of these fungi the acidity next the fungus colony was tested by applying a piece of indicator paper to the agar. A similar test at the edge of the dish enabled us to approximate the change produced by the fungus. In some instances the indicator paper was supplemented by applying drops of indicator solution to the agar. Most of the fungi which were found by these tests to form considerable acid also developed a zone of precipitation in the medium adjacent to the colony.

As a rule the inhibition of *Staph. aureus* exceeded that of *E. coli*. Again there are exceptions on both media and almost all of these were fungi which produced a great deal of acid. Example, *Poria luteofibrata* (B).

Thirty-six of the fungi were observed to inhibit *Staph. aureus* on the thiamine-peptone agar but to have no or a slight (1 mm.) effect on *E. coli*. Example, *Corticium abeuns*. On malt agar this was observed for 40 of the 119 fungi.

With 40 of the fungi an inhibition of *Staph. aureus* was observed on the thiamine-peptone agar, but none or a slight inhibition (1 mm.) on malt agar. Example, *Corticium lividum* (5159).

While some strains of the same species showed similar responses, among strains of other species considerable differences were observed. See the 6-day-old cultures of *Poria luteofibrata*.

Usually the antibiotic activity increased with the age of the fungus colony, but in some instances it decreased. See *Fomes applanatus* (59054-S).

The character of the inhibition varied. Five types were distinguished as follows: The bacterial streak ended in a sharp distinct line; the streak gradually faded out; the streak ended with a sharp break but isolated colonies appeared between the break and the fungus colony; the streak ended with a sharp break but faint growth gradually fading out continued toward the fungus colony; the streak ended with a sharp break and faint but uniform growth continued up to the fungus colony.

**Results with Dermatophytes on Streak Plates.** Of the dermatophytes tested 18 showed no inhibition or little inhibition (6 mm. or less) when tested after from 3 to 19 days, depending upon the rapidity of growth. These were *Achorion schoenleini* 4822 (ATC), *A. schoenleini* 2044 (NIH), *Epidermophyton inguinale* (RB), *Microsporum felineum* (RB), *M. felineum* 8137 (ATC), *M. gypsum* (RB), *Trichophyton crateriforme* (RB), *T. gypsum*, *T. gypsum* 2035 (NIH), *T. gypsum* (RB), *T. interdigitale* 4807 (ATC), *T. interdigitale* 4808 (ATC), *T. mentagrophytes* V10 (NIH), *T. purpureum* AMS-3 (NIH), *T. rosaceum* (RB), and *T. tonsurans* V13 (NIH), *T. violaceum* 2034 (NIH), 8532 (ATC) and (RB).

Four of the dermatophytes gave zones of inhibition of 10 mm. or more (table 1) for *Staph. aureus*. *Epidermophyton inguinale* (RB) was quite active on malt agar, and *Microsporum canis* (650-ATC) inhibited *Staph. aureus* on malt but not on thiamine-peptone agar. None was active for *E. coli*.

**The Disc Method.** The determination of antibiotic activity by the streak method described above is useful chiefly in eliminating a considerable number of the fungi included in a survey. It is possible that those organisms tested by the streak method which evidenced no antibiotic activity, or little activity, when grown on the thiamine-peptone medium, or on 2 per cent malt, would produce antibiotic material effective against the test bacteria if grown on other media, or under other conditions. It is possible also that the fungi inactive against *Staph. aureus* and *E. coli* form substances antibiotic for other organisms. Furthermore, the streak method as used here would not detect organisms which formed antibiotic substances and retained them within the hyphae. However, from a practical standpoint in this survey it seemed most profitable to select for more detailed examination some of

TABLE 1. Antibiotic activity of fungi tested by streak method  
Zone of inhibition over 10 mm. (p) indicates partial inhibition. See text for details.

Fungus	Age of colony days	Malt agar			Thiamine-peptone agar			Acidity
		Radius colony mm.	Inhibition mm.		Radius colony mm.	Inhibition mm.		
			<i>Staph. aureus</i>	<i>E. coli</i>		<i>Staph. aureus</i>	<i>E. coli</i>	
<i>Claudiopeus nidulans</i> (71364-S)	9	17	9	0	10	13	0	.....
	15	19-28	3	0	22-25	25	4	.....
<i>Coniophora cerebella</i> (94042-R)	6	11	5	5	8	25	26	.....
	9	17	0	0	9-18	40	33	A
<i>C. suffocata</i> (56488-S)	5	20	6-7	1	18	13	9	.....
	6		8	1	12	12	12	.....
<i>Corticium abeuns</i> ? (14572)-R	6	8	29	0	10	29	0	.....
	6	7.5	34	0	10	25	0	.....
<i>C. conigenum</i> (66211-Sp)	4	13	5	0	12	7	1	.....
	6	28	0	0	25	11	0	.....
<i>C. hydnans</i> (57407-S)	6	10	16	2	7	31	12	.....
	10	18	21	5-6	11	43	21	.....
<i>C. lividum</i> (5159)	7	26	0	0	7	15	10	.....
	7	34	0	0	5	20	10-13	.....
<i>C. lividum</i> (15084-R)	6	30	0	0		32	26	.....
	15					27	10-15	.....
<i>Daedalea heteromorpha</i> (59051-R)	6	5.5	21	0	5.5	27	27	A
	9	15	7-11	20	13	45	27	.....
<i>D. juniperina</i> (71585-R)	6	10	10	6(p)	10	20	15(p)	.....
	9	21	11	10(p)	19	31	25(p)	A
<i>D. quercina</i> (57076-S)	5	13	6	0	12	15	8	.....
	6		10	8(p)		20	19-20	A
<i>Fistulina hepatica</i> (1818)	7		0	0		3	0	.....
	14	18	0	0	12	26	0	.....
<i>Flammula alnicola</i> (2071)	6	15	4	0	12	19	11	.....
	11	24	9	3	15-18	36	21	.....
<i>Fomes annosus</i> (58548-S)	6	32	5	0	29	20-27	0	.....
	6	37	3	0	25	10-15	0	.....
<i>F. applanatus</i> (59054-S)	7	6	0	0	6	10-12	10-15	.....
	10	10	0	0	9	3(p)	0	.....
<i>F. ferruginosa</i> ? (H-43)	10	2-4	0	0	2-4	11	0	.....
	19	10	0	0	9	0	0	.....
	8	10	0	0	16	13	0	.....
<i>F. fraxinophilus</i> (59120-S)	13	13	0	0	15	12	0	.....

TABLE 1 (continued)

Fungus	Age of colony days	Malt agar			Thiamine-peptone agar			Acidity
		Radius colony mm.	Inhibition mm.		Radius colony mm.	Inhibition mm.		
			<i>Staph. aureus</i>	<i>E. coli</i>		<i>Staph. aureus</i>	<i>E. coli</i>	
<i>F. fraxinophilus</i> (B)	6	15	0	0	12	9	0	..
	9	28	0	0	15	20	8	..
<i>F. juniperinus</i> (72028-S)	13	8	28	18	6	41	35	..
	19	8	32	25	7	5	1	..
<i>F. juniperinus</i> (CBS)	13	9	14	6	7	27	22	..
	13	9	13	6	7	28	22	..
<i>F. meliae</i> (50336-R)	4	13	8	3	12	20	15	..
	8	25-28	13	5	17-19	35	25	A
<i>F. officinalis</i> (80518-S)	10	8-9	10-12	3(p)	5	28	12	..
	13	10	21	4	8	50	27	A
<i>F. pini</i> (52061-S)	6	10	3	0	8	18	10	..
	8	13	6	5	10-11	26	15	..
<i>F. pini</i> var. <i>abietis</i> (71112)	8	12	0	0	9	7	0	..
	10	15-17	5-6	1-2	13-14	21	12	A
<i>F. pinicola</i> (59017-S)	6	15	5	0	15	28	25	..
	8	23	13	5	22	37	32	A
<i>F. ribis</i> (94142)	10	7	10(p)	0	10-11	15	0	..
	13	10	8	0	12	46	0	..
<i>F. ribis</i> (CBS)	5	16	0	0	13	6	3	..
	6	16	2	0	13	12	3	..
<i>F. roseus</i> (10)	6	8	5	0	13	13	10(p)	..
	8	15	0	0	22	12	2(p)	..
<i>F. subroseus</i> (20)	4	10	0	0	9	17	10	..
	6	20	0	0	19	23	18	A
<i>F. tenuis</i> (58528-R)	10	8-9	0	0	5-9	10	0	..
	13	11	0	0	10	11	0	..
<i>F. ulmarius</i> (CBS)	7	8	0	0	4	40	36	..
	10	8	0	0	4	20-25	18(p)	A
<i>F. ungulatus</i> (CBS)	6	24	10(p)	4(p)	10	28	25	..
	8	27	10	9	15	40	30	A
<i>Ganoderma</i> sp. (86194)	4	15	0	0	9	9	0	..
	6	29	0	0	20	13	0	..
<i>Hirneola</i> sp. (Iowa 42)	6	..	0	0	..	0	0	..
	14	..	..	..	..	18	2	..
<i>Hydnium abietis</i> † (3548)	16	14	22	0	6	44	1	..

TABLE 1 (continued)

Fungus	Age of colony days	Malt agar		Thiamine-peptone agar		Acidity		
		Radius colony mm.	Inhibition mm.		Radius colony mm.		Inhibition mm.	
			<i>Staph. aureus</i>	<i>E. coli</i>			<i>Staph. aureus</i>	<i>E. coli</i>
<i>H. caput-ursi</i> (71748)	7	14	0	0	9-11	14	8	
	16	17-28	8	5	13-19	20	14	
<i>H. scheidermayeri</i> (71787-R)	7		6	0		28	3(p)	
	14	18-22	3(p)	0	8	40	15(p)	
<i>H. septentrionale</i> (52037-S)	7	18	4	0	12	13	0	
	16	35	6	0	25-28	20	6	
<i>H. septentrionale</i> (72067)	7	18	0	0	13	4	0	
	7	18	0	0	13	15	0	
	5	13	7	2-3(p)	14	13	4-5(p)	
<i>Hymenochaete corrugata</i> (71759-R)	6					15	7(p)	
<i>H. rubiginosa</i> (58557-R)	5	4	0	0				
	14	17	0	0	6-7	30	0	
<i>H. rubiginosa</i> (58512-R)	6	15	3(p)	0		3	0	
	14	16	5	0	16-17	20	0	
<i>H. tabacina</i> (71248-R)	5	16	0	0	13	10-12	4(p)	
	6		0	0		10	5(p)	
<i>Hypholoma sublateritium</i> (56468-S)	6	10	5	0	9	9	0	
	6	22	3	0	20	11	0	
<i>Irpex cinnamomeus</i> (67937)	11	11	0	0	10	7	2	
	6	17	0	0	15	16	5	
<i>I. mollis</i> (71542-R)	6		15	0		25	1	
	9	35-40	0	0	45	0	0	
<i>Ithyphallus</i> sp. (S-1)	9	13	0	0	10	9(p)	4(p)	
	15	21-22	0	0	17-20	27	10	
<i>Lenzites sacpiaria</i> (13812)	6	21	0	0	20	10	0	
	9	26	3	0	30	13	5	
<i>Lepiota naucina</i> (312)	9	17	13	8	10	18	13	
	15	23-27	9	4	16-22	22	9	
<i>Omphalia campanella</i> (94075-R)	15	12	3	0	7	14	0	
	22	20	1-2	0	14	12	0	
<i>Panus stipticus</i> (71518-Sp)	6	10	10	0	10	6	0	
	11	23	4	0	20	12	0	
<i>P. stipticus</i> (luminous) (CBS)	9	7	2	0	8	9	0	
	15	16	0	0	18	11	0	
<i>Parillus involutus</i> (94261-S)	10	3-3.5	6	0	11-14	9	0	
	13	3	0	0	10	16	0	

TABLE 1 (continued)

Fungus	Age of colony days	Malt agar			Thiamine-peptone agar			Acidity
		Radius colony mm.	Inhibition mm.		Radius colony mm.	Inhibition mm.		
			<i>Staph. aureus</i>	<i>E. coli</i>		<i>Staph. aureus</i>	<i>E. coli</i>	
<i>Phlebia strigosozonata</i> (56454-S)	4	13	0	0	10	15	0	
	6		0	0		25	5	
<i>Pholiota aeruginosa</i> (1997)	6	13	0	0	11	11	0	
	9	22	0	0	17	3	0	
<i>Pleurotus griseus</i> ? (14616-R)	9	7-9	14-17	0	5	26-30	0	
	15	19	8-16	0	14	43-48	0	
<i>Polyporus albellus</i> (14554-S)	4	18	0	0	18	12	0	
	6	27	0	0	26	12	0	
<i>P. alboluteus</i> (72163)	5	24	0	0	27	15	0	
	6	30	0	0	32	8	0	
<i>P. balsameus</i> (71191-R)	6	11	0	0	11	20	10	
	10	26	0	0	22	29	22	A
<i>P. betulinus</i> (58514-S)	5	34	0	0	23	9	5	
	6	40	0	0	27	12	0	A
<i>P. biformis</i> (71423-R)	5	27	12	9	27	15	3	
	6	34	13	2	27	15	3	
<i>P. delectans</i> (71089)	7	15	6	0	13	25	0	
	16	44	0	0	17	22	0	
<i>P. dureseus</i> (71096)	4	17	7	5	16	29	26	
	5	23	10	10	20	30	23	A
<i>P. fragilis</i> (71326-S)	7	10	7	0	6	32	27	
	10	13	10	5	9	45	40	A
<i>P. fumidiceps</i> (59064-S)	5	28	0	0	25	9	0	
	6	32	0	0	30	11	0	A
<i>P. galactinus</i> (52034-S)	6	25	0	0	20	13	0	
	7	43	0	0	37	9	0	
<i>P. giganteus</i> (50382-R)	7	11	5	0	14	16	0	
	10	15	18	0	8-9	26	0	
<i>P. giganteus</i> (57026)	10	8	12	0	5-6	15	7	
	14	12	9	0	8	25	0	
<i>P. guttulatus</i> (71799-S)	6	5	0	0	3	0	0	
	10	14	2	0	9	18	10	A
<i>P. immitus</i> (71384)	7	16	8	3	23	30	23	
	10	36	9	7	24	32	32	A
<i>P. obtusus</i> (71791-S)	6	13	8	0	7	21	16	
	10	33	7	0	19	17	0	

TABLE 1 (continued)

Fungus	Age of colony days	Malt agar				Thiamine-peptone agar				Acidity
		Radius colony mm.	Inhibition mm.		Radius colony mm.	Inhibition mm.				
			<i>Staph. aureus</i>	<i>E. coli</i>		<i>Staph. aureus</i>	<i>E. coli</i>			
<i>S. rugosum</i> (86351)	8	6	17	0	6-8	10	0	.....		
	13	9	26	0	13	32	4	.....		
<i>S. subpileatum</i> (50230-R)	4				3	0	0	.....		
	12	25	0	0	6-8	11-15	7	.....		
<i>S. sulcatum</i> (71329-R)	4	4	0	0	4	0	0	.....		
	12	13-14	14	6	9	14-17	10	.....		
<i>Trametes alaskani</i> (B)	11	18	0	0	8	11	5	.....		
	15	28	0	0	18	15	5	A		
<i>T. americana</i> (18125-R)	6	12	0	0	13	15	6	.....		
	9	21	3	0	21	14	6	.....		
<i>T. carnea</i> (571)	4	14	0	0	9	6(p)	0	.....		
	6	24	5	0	17	17	7	A		
<i>T. heteromorpha</i> (71189-S)	6	15	10	0	15	37	30	.....		
	9	21	12	13	22	44	40	A		
<i>T. malicola</i> (71956)	6	12	4	0	12	25	11	.....		
	9	22	0	0	18	33	27	A		
<i>T. malicola</i> (B)	6	12	22	22	8	45	37	.....		
	9	14	21	23	11	52	50	A		
<i>T. rubescens</i> (H-61)	6	14	12	0	12	23	0	.....		
	9	26	12	0	18	24	0	.....		
<i>T. sepium</i> (71876-S)	4	11	9	6	10	19	10-15	A		
	6	18	11	11	18	35	26	.....		
<i>T. serialis</i> (94023)	6	15	5	0	13	13	7	.....		
	9	25	0	0	14	26	17	A		
DERMATOPHYTES										
<i>Epidermophyton inguinale</i> (RB)	10	6-10	10	0	12-14	3	0	.....		
	14	15	18	0	18	26	0	.....		
<i>Microsporum canis</i> (650-ATC)	7	17	17	0	21	0	0	.....		
	10	26	17	0	31	0	0	.....		
<i>Trichophyton purpureum</i> (8531-ATC)	10	12	0	0	13	5	0	.....		
	14	15	2(p)	0	17	15(p)	0	.....		
<i>T. purpureum</i> (RB)	10	10	2	0	11-12	9	0	.....		
	14	10	6	0	13	10-17	0	.....		



those fungi which had been found by the streak method to be most active. Forty-four of the fungi in table I were chosen for further experimentation chiefly because of their activity against *Staph. aureus* on thiamine-peptone agar and of their failure to produce extreme acidity. We included also *Ceratostomella ulmi*, *C. rostracylindrica*, *Epicoccum* sp., and *Stereum murrayi* (71162).

A modification of a method described by Raper, Alexander and Coghill (3) was used for this group. It consisted in growing the fungus on an agar medium in Petri dishes. At intervals after inoculation discs of agar were cut on a radius extending from the center of the colony to the edge of the dish. The discs were transferred to another agar plate seeded with the test organism. The diameter of the zone of inhibition produced by antibiotic material diffusing from the disc was measured. We used 20 ml. of various agar media<sup>7</sup> in a Petri dish, 15 × 100 mm., for cultivating the fungus which was inoculated in the center of the dish and incubated at 25° C. A cork borer 5.5 mm. in diameter was used for cutting the discs. Eighteen ml. of a yeast-peptone medium were poured into a Petri dish and allowed to stand overnight. This was then coated with 7 ml. of the same medium to which were added 0.2 ml. of a 24-hour broth culture of the test bacteria diluted in the proportion of 1.2 ml. of the culture to 10 ml. of sterile beef broth. When the coating layer had solidified the discs were transferred and the plates incubated upside down at 37 ± 2° C. Evidence of antibiotic activity could be observed after 5 or 6 hours, but final observations were made after 24 hours. The growth of both *Staph. aureus* and *E. coli* was considerably heavier on the yeast-peptone agar than on the thiamine-peptone agar.

**Results with the Disc Method.** The activity as determined by the disc method was classified as none (0), little (+), minor (++) , medium (+++) , and strong (++++). The strongest activity was not so great as that found for *Penicillium notatum* (P832C).

When grown at 25° C on thiamine-peptone agar little or no activity was found for *Ceratostomella ulmi*, *C. rostracylindrica*, *Claudopus nidulans* (71364-S), *Coniophora suffocata* (56488-S), *Corticium lividum* (5159), *Flammula alnicola* (2071), *Fomes ulmarius* (CBS), *Hydnum scheidermayeri* (71787-R), *Hymenochaete corrugata* (71759-R), *H. rubiginosa* (58557-R), *Polyporus tulipiferus* (71938), *P. vulpinus* (2279), *Poria incrassata* (59125-

<sup>7</sup> These included the thiamine-peptone agar; a yeast-peptone medium which contained per liter 5.0 g. neopeptone, 3.0 g. yeast extract, 1.0 g. dextrose, and 15 g. Difco agar (the pH of this medium was 6.6); modified Dox plus corn steep water solids (C. M. Armstrong, Inc.) which contained per liter 3 g. NaNO<sub>3</sub>, 1 g. KH<sub>2</sub>PO<sub>4</sub>, 0.5 g. KCl, 0.5 g. MgSO<sub>4</sub> · 7H<sub>2</sub>O, 0.01 g. Fe<sub>2</sub>(SO<sub>4</sub>)<sub>3</sub>, 40 g. dextrose, 5 g. corn steep water solids, and 15 g. Difco agar; starch-tryptone agar which contained per liter 10 g. soluble starch, 5 g. tryptone, 1.5 g. KH<sub>2</sub>PO<sub>4</sub>, 0.5 g. MgSO<sub>4</sub> · 7H<sub>2</sub>O, the mineral supplements previously mentioned, and a mixture of pure B complex vitamins.

R), *P. subacida* (B), and *Stereum murrayi* (71162), and only minor activity for *Fomes annosus* (58548-S), *Polyporus albellus* (14554-S), *P. resinosis* (52043-S), *P. schweinitzii* (71356-S), *Poria ferruginea-fusca* (1411), *P. sequoiae* (F-8755), and *Stereum sulcatum* (71329-R). These fungi were not grown on other media for test by the disc method. *Fomes juniperinus* (72028-S and CBS) and *F. ribis* (94142) showed little or no activity when grown on the thiamine-peptone medium, the Dox medium supplemented with

TABLE 2. Degree of antibiotic activity in the agar disc method with the following media: thiamine-peptone agar, modified Dox plus corn steep water solids, and yeast-peptone agar

Degrees of activity: 0 = none; += little; +=+ minor; +++ = medium; ++++ = strong.

Fungus	Degree of activity on		
	Thiamine-peptone	Dox medium plus corn steep solids	Yeast-peptone
<i>Corticium abrams</i> ? (14572-R) ..	++++	++++	0
<i>C. hydnans</i> (57407-S) ..	+++	+++	0
<i>Epicoecum</i> sp. ....	+++	..	
<i>Hydnium abietis</i> ? (3548) ..	+++		
<i>H. septentrionale</i> (52037-S) ..	++++	++++	
<i>Irpex mollis</i> (71542-R) ..	++++	++++	
<i>Lepiota naucina</i> (312) ..	+	+++	0
<i>Phlebia strigosozonata</i> (56454-S) ..	+++	+++	0
<i>Pleurotus griseus</i> ? (14616-R) ..	+++	+++	0
<i>Polyporus biformis</i> (71423-R) ..	++++	++++	
<i>P. delectans</i> (71089) ..	++++	++++	
<i>P. giganteus</i> (50382-R) ..	++	0	0
<i>P. giganteus</i> (57026) ..	+++		
<i>P. obtusus</i> (71791-S) ..	++++	++++	
<i>P. radiatus</i> (B) ..	+++		
<i>P. trabeus</i> (55196-R) ..	++	++	
<i>Poria corticola</i> ? (71280-R) ..	+	++++	+++
<i>P. subacida</i> (71155) ..	++++	++++	++
<i>P. tenuis</i> (67942) ..	++++	++++	++++
<i>Radulum orbiculare</i> (57402-S) ..	+++	+	0
<i>Stereum gausapatum</i> (58581) ..	++	++	+
<i>S. rugosum</i> (86351) ..	0	++	0
<i>Trametes rubescens</i> (H-61) ..	++	+	0

corn steep water solids, and on the yeast-peptone medium. The results with the remaining 23 of the 48 fungi tested by the disc method are given in table 2.

In several instances the correlation between the results obtained with the streak method and the disc method was poor, i.e., considerable inhibition was observed with the streak method but no, or little, activity with the disc method of investigation. It is probable that this difference occurred because the antibiotic substance diffused widely in the agar on which the fungus grew, but did not accumulate in sufficient amount to produce an effect when discs were removed and tested on a fresh medium. There are other possible expla-

nations, some of which were examined for *Fomes ribis* (94142), one of the organisms which evidenced considerable activity against *Staph. aureus* by the streak method but none when tested by the disc method (fig. 1, A and B). The streak tests were carried out on the thiamine-peptone agar, the medium

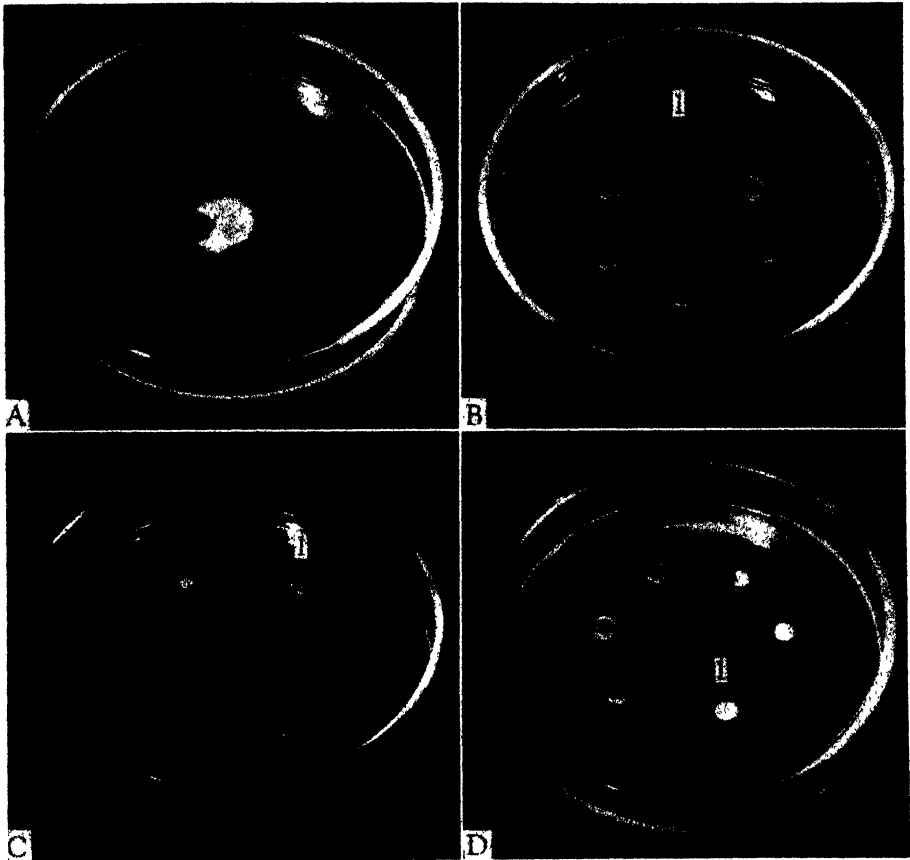


FIG. 1. A, antibiotic activity of 7-day-old *Fomes ribis* (94142) tested by streak method on thiamine-peptone agar. *Staph. aureus* largely inhibited, *E. coli* not affected. B, tested by disc method, no antibiotic activity against *Staph. aureus*. C, complete inhibition of *Staph. aureus* with stimulation of bacteria at edge of inhibited zone. Discs from colony of *Pleurotus griseus* (14616-R) grown 17 days on modified Dox medium plus corn steep water solids. D, partial inhibition of *Staph. aureus*. Discs from *Poria tenuis* (67942) grown 14 days on modified Dox medium plus corn steep water solids. The number, 1, marks the disc taken nearest the center of the colony.

on which the fungus grew; the discs were tested on the yeast-peptone medium. However, we found little or no activity for the discs from a culture of *Fomes ribis* when tested on the thiamine-peptone medium. We found further that the difference between the streak method and the disc method for

this fungus was not the result of slow diffusion of the antibiotic substance from the disc, or to a lack of stability of the antibiotic substance at  $37 \pm 2^\circ \text{C}$ .

The medium on which the fungus was grown markedly affected the formation of antibiotic material. For example, we observed little antibiotic activity of *Penicillium notatum* grown on thiamine-peptone agar, of *Poria corticola* (71280-R) on a starch-tryptone or thiamine-peptone medium, of

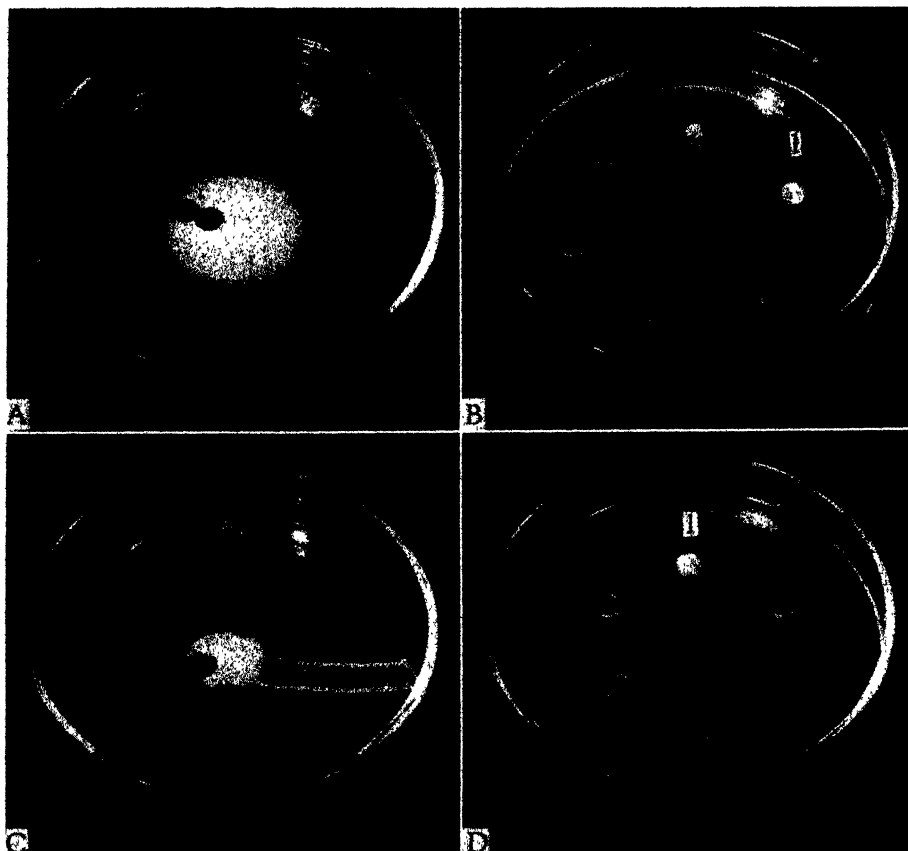


FIG. 2. Effect of medium on production of antibacterial material. A, *Corticium abeuns* (14572-R), 17 days old, on Dox medium plus corn steep water solids. *Staph. aureus* completely inhibited, *E. coli* partially. B, discs from A tested against *Staph. aureus*. Complete inhibition with resistant colonies. C and D, same as A and B, but fungus grown on yeast-peptone agar. No inhibition of streaks and no antibiotic action with discs. The number, 1, marks the disc taken nearest the center of the colony.

*Corticium abeuns* (14572-R) (fig. 2) and *Pleurotus griseus* (14616-R) on a yeast-peptone medium. In general, the modified Dox medium plus corn steep water solids was the most satisfactory medium for the production of antibacterial substances by these fungi (table 2).

It was not possible to predict from the results obtained with one fungus the effect of a particular medium on the antibiotic activity of another mold. For example, the yeast-peptone medium was quite satisfactory for *Poria tenuis* (67942) and for *Penicillium notatum*; it was poor for *Poria subacida* (71155), and no antibiotic activity of *Corticium abeuns* (14572-R) and *Pleurotus griseus* (14616-R) was observed on this medium when the disc method was used.

Two types of antibiotic action were observed as follows:

(1) The antibiotic material diffusing out from the disc completely inhibited the bacteria; the disc was surrounded by a sharply defined clear ring. In some instances the growth of the bacteria at the edge of the ring appeared to be stimulated (fig. 1, C). This type of inhibition appeared to be bactericidal in character and is referred to as "complete."

(2) The antibiotic material held back the growth of the bacteria in the vicinity of the disc but did not eliminate it completely; the area of inhibition appeared cloudy because of the presence of numerous small bacterial colonies (fig. 1, D). This type of inhibition is called "partial," and was bacteriostatic rather than bactericidal. Frequently with this type the disc was surrounded by zones of inhibition alternating with zones in which the inhibition was less marked. This gave the area of bacteriostatic activity the appearance of a bull's-eye or of Liesegang rings.

Between these two clearly marked types various intermediates were observed. For example, we found in some instances a narrow zone of complete inhibition surrounded by a broader zone of partial inhibition, and a type in which the area of inhibition contained a considerable but reduced number of colonies of somewhat larger size than those which developed in the balance of the plate.

These differences in types of antibiotic action indicate differences in the kind or in the amount of antibiotic and perhaps stimulating substances produced by the various fungi.

For some of the fungi the antibiotic activity of discs taken from within the limits of the mycelium decreased with time; the disc with greatest antibiotic activity was that at or near the edge of the colony. This occurred with *Poria corticola* (71280) and *Poria subacida* (71155) (fig. 3, B). For other fungi the antibiotic activity persisted and increased within the mycelium; the disc with greatest antibiotic activity was that nearest the center of the fungus colony. This was especially marked with *Corticium abeuns* (14572-R) (fig. 3, A and fig. 2, B) and *Poria tenuis* (67942) (fig. 3, D).

The antibiotic activity did not increase with increased rapidity of growth when a fungus was grown on different media on which rates of growth differed. It was not greater with those species of fungi which grew more rapidly as compared with those which grew less rapidly. In fact, it appeared in many

instances that the correlation between growth and antibiotic activity, as measured by the disc method, was negative. Many of the fungi which grew rapidly showed little or no antibiotic activity (or the action could be accounted for by acid production), and a particular fungus might evidence little antibiotic activity on a medium on which it grew well and considerable on one on which it grew poorly (fig. 4).

The antibiotic material from some of the fungi tested diffused beyond the limits of the mycelium; discs 1.5 or 2.0 mm. from the edge of the colony

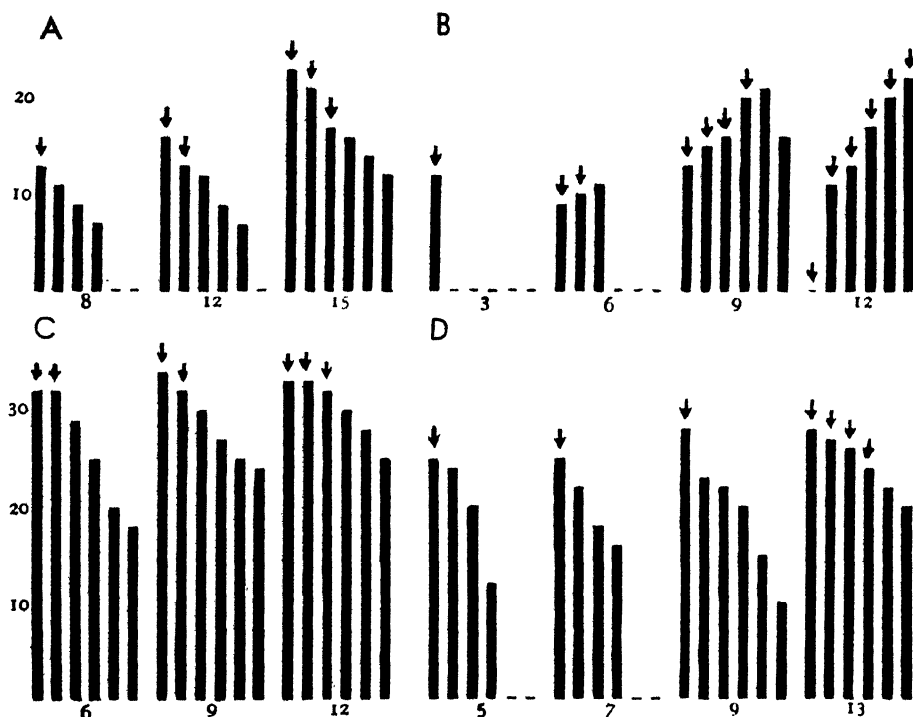


FIG. 3. Diameter in mm. of inhibition zones for *Staph. aureus* produced by discs from various fungi. Each test includes 6 discs taken from center of colony outward. All fungi grown on Dox medium plus corn steep water solids. The arrows show those discs which came from the fungus colony. A, *Corticium abeuns* (14572-R), 8, 12, 15 days old; B, *Poria subacida* (71155), 3, 6, 9 and 12 days old; C, *Penicillium notatum* (P832C1), 6, 9 and 12 days old; D, *Poria tenuis* (87942), 5, 7, 9 and 13 days old.

were active (fig. 3, D). With other fungi the only active discs were those removed from within the colony. For example, discs from the colony of *Hydnum septentrionale* (52037-S) were strongly active, producing zones of complete inhibition with a diameter of as much as 24 mm. However, discs taken from outside the limits of the colony were inactive. The reasons for this are not clear. It may indicate that the antibiotic material is largely retained by the mycelium and not freed until the discs are cut and incubated at

$37 \pm 2^\circ \text{C}$ . We were not successful in releasing the material by incubating uninjured colonies of the fungus at the higher temperature.

The observations on the more active fungi tabulated in table 2 were as follows:

*Corticium abeuns* (14572-R) grew with medium rapidity; the inhibition

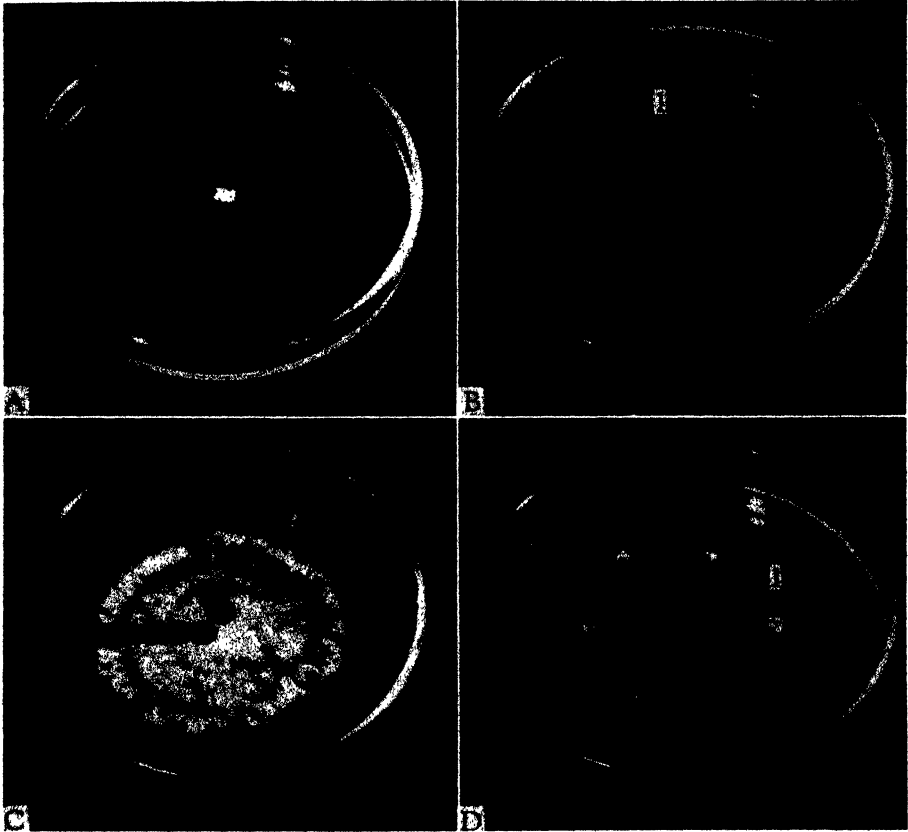


FIG. 4. An extreme example of negative correlation between growth and antibiotic activity. *Pleurotus griseus* (14616-R) grown: A, 21 days on a thiamine-peptone agar with 100 g. dextrose per liter; B, discs from A on plate seeded with *Staph. aureus*; C, 19 days on Dox medium plus corn steep water solids and 20 g. brown sugar per liter; D, discs from C on plate seeded with *Staph. aureus*. The number, 1, marks the disc taken from nearest the center of the colony.

was complete with scattered resistant colonies; the antibiotic material diffused widely and persisted within the colony (fig. 2, B).

*C. hydnans* (57407-S) resembled *C. abeuns* but was less active.

*Epicoccum* sp. grew rapidly; the inhibition was complete; the antibiotic material did not diffuse much beyond the limits of the colony and decreased within the colony.

*Hydnum abietis*? (3548) grew slowly; the inhibition was complete; the antibiotic material diffused widely and decreased with time within the colony.

*H. septentrionale* (52037-S) grew with medium rapidity; the inhibition was complete; the antibiotic material did not diffuse beyond the colony and persisted within the colony.

*Irpeex mollis* (71542-R) grew rapidly; the inhibition was complete becoming partial with age on the thiamine-peptone medium; the antibiotic material diffused widely and persisted well within the colony.

*Lepiota naucina* (312) grew with medium rapidity; the inhibition was complete; the antibiotic material was limited to the colony and persisted well within the colony.

*Phlebia strigosozonata* (56454-S) grew slowly; the inhibition was complete; the antibiotic material diffused beyond the colony and persisted well within the colony.

*Pleurotus griseus* (14616-R) grew with medium rapidity; the inhibition was complete; the antibiotic material diffused widely and persisted within the colony (fig. 1, C).

*Polyporus biformis* (71423-R) grew rapidly; the inhibition was variable in type; the antibiotic material was largely limited to the colony and tended to decrease within the colony with time.

*P. delectans* (71089) grew rapidly; the inhibition was complete; the antibiotic material was largely confined to the colony and persisted well within the colony.

*P. obtusus* (71791-S) resembled *P. delectans* (71089).

*P. radiatus* (B) resembled *Corticium hydnums*.

*Poria corticola*? (71280-R) grew rapidly; the inhibition was largely partial; the antibiotic material diffused widely and decreased within the colony with age.

*P. tenuis* (67942) grew with medium rapidity; the inhibition was mainly partial; the antibiotic material diffused widely and persisted well within the colony (fig. 1, D).

*P. subacida* (71155) grew rapidly; the inhibition was mainly partial; the antibiotic material was mainly confined to the colony and decreased within the colony with age (fig. 3, B).

*Radulum orbiculare* (57402-S) grew slowly; the inhibition was complete; the antibiotic material diffused widely and persisted well within the colony.

*Stereum gausapatum* (58581) grew with medium rapidity; the inhibition was complete; the antibiotic material diffused widely and persisted within the colony.

**Serial Dilution Method.** Although the disc method has certain advantages, its usefulness is limited to cultures in which the fungus is grown on



a semisolid medium. If it is desired to test the antibiotic agent on animals, or to concentrate and perhaps isolate it, culture liquids are necessary unless the agent can be extracted from the mycelium. A convenient method of testing the activity of culture liquids is to determine the action of a series of dilutions on the growth of the test bacterium. Our procedure was as follows:

The fungus was grown in flasks at 25° C until a mycelial mat had formed over the surface of the culture liquid. At various intervals after the mat had formed the old culture liquid was poured off and replaced with fresh culture fluid, the antibiotic activity of which was tested after 1, 3, and 5 days contact with the mycelial mat. For some mats this process was repeated several times.

For the serial dilutions 1 ml. of a 6-hour broth culture of *Staph. aureus*, which had been diluted 1 to 100,000 with beef broth, was placed in standard tubes, 10 × 75 mm. To the first tube 1 ml. of the culture fluid (neutralized if necessary) was added, giving a dilution of 1 to 2. One ml. from this tube was transferred to the second tube, giving a dilution of 1 to 4. This was continued for a set of 10 or more tubes. The tubes were incubated for 24 hours at 37 ± 2° C and examined for bacterial growth.

**Results with Serial Dilutions.** With a few exceptions the antibiotic activity of culture liquids from the fungi we examined was unsatisfactory. For *Corticium abeuns* (14572-R), *Fomes juniperinus* (CBS and 72028-S), *Fomes ribis* (94142), *Lepiota naucina* (312), *Polyporus giganteus* (50382-R and 57026), *Poria ferruginia-fusca* (1411), *P. subacida* (71155), *Radulum orbiculare* (57402), *Stereum rugosum* (86351), *S. sulcatum* (71329-R), and *Trametes rubescens* (H61) the maximum activity did not surpass dilutions of 1 to 64, and in many instances was less. With *Poria corticola* (71280-R) and *P. tenuis* (67942) culture fluids active at a dilution of 1 to 256, and for *Pleurotus griseus* (14616-R) and *Irpex mollis* (71542-R) culture liquids active at a dilution of 1 to 1024 were obtained. Mats of *Pleurotus griseus* which were 50 days old were still effective in producing antibiotic material.

#### DISCUSSION

A considerable proportion of the wood-destroying fungi included in this survey showed antibiotic activity, and for most of these it appeared to be caused by other substances than the hydrogen-ion. Antibiotic activity was not confined to particular genera. One or more species of 43 of the 72 genera included in this survey showed some antibiotic activity. Several of the genera which showed no activity were represented in our survey by a single species. Of the 94 species and isolations of *Polyporus* studied by the streak method, 51 were inactive, 19 gave inhibitions of 10 mm. or less, and 24 of 11 mm. or more. Of the 24, we considered the antibiotic activity of 11 to be caused by acid production. Of the 47 *Fomes* surveyed, 15 gave negative results; 13,

inhibitions of 10 mm. or less; and 19, of 11 mm. or more. The antibiotic activity of 7 of the 19 was probably the result of acid production. Of 41 *Porias* studied, 9 were inactive and 19 produced inhibitions of 11 mm. or more. The antibiotic activity of 11 of the 19 was probably caused by acid formed by the fungi.

In many instances the different isolations of a species were alike in antibiotic activity. For example, 2 isolations of *Polyporus anceps* were both negative, two isolations of *P. circinatus* were slightly antibiotic. On the other hand, although the two isolations we tested of *P. delectans* were alike morphologically, one was negative and one was strongly antibiotic.

However, in some respects the results of the investigation were disappointing. None of the more than 400 fungi investigated was as effective as *Penicillium notatum* in producing material active against *Staph. aureus*, and although some inhibited *E. coli*, none affected the gram-negative bacterium as much as the gram-positive, except in those instances in which the inhibition appeared to be caused by acidity.

It might be recalled, however, that the culture liquids of *Penicillium notatum* with which Fleming initiated his investigations of that organism were effective against *Staph. aureus* at a dilution of 1 to 800 (1). By modifying the cultural conditions and the composition of the culture liquid it has been possible to increase this activity several times. In our experiments culture liquids were obtained from *Pleurotus griseus* which were active at a dilution of 1 to 1000 and from *Poria corticola* and *Poria tenuis* active at a dilution of 1 to 250. Whether the activity of these fungi also can be materially increased by selection of strains, or by modification of cultural conditions, can only be determined by further research. In addition, we have not in this survey investigated the possibility that antibacterial agents may be present in the mycelium and not released into the culture fluid.

Some miscellaneous observations were made in the course of our survey which suggest that the antibiotic agents produced by some of these fungi are not penicillin, and that the substances formed by some, at least, of the fungi studied are not identical. For example, the character of the area of inhibition around the blocks differed. *Corticium abeuns* produced complete inhibition with many resistant colonies toward the edge of the clear area. *Pleurotus griseus* completely inhibited *Staph. aureus*, but the resistant colonies so characteristic for *Corticium abeuns* were absent. For both of these fungi the edge of the clear area was sharply defined and lacked the transition zone of partially inhibited colonies noted with *Penicillium notatum*. *Poria corticola* (71280-R), *P. subacida* (71155), and *P. tenuis* (67942) all showed partial inhibition clearly distinguishable from the action of *Penicillium notatum*, *Corticium abeuns*, and *Pleurotus griseus*. Of the three species of *Poria* the activity of *P. tenuis* could be distinguished from that of the other

two by the persistence of antibiotic activity within the colony. From these six fungi there appeared to be at least four and perhaps five different antibiotic agents. Of course at the present stage of our investigations we have no evidence on whether the activity of any one of the wood-destroying fungi results from one or more than one antibiotic agent.

The antibiotic material produced by *Corticium abeuns* was distinguished from penicillin and streptothricin by testing against penicillin and streptothricin a strain of *Staph. aureus* resistant to the antibiotic material produced by this fungus. Strains of *Staph. aureus* resistant to the action of *Corticium abeuns* were isolated from resistant colonies in the vicinity of discs taken from the fungus (fig. 2, B). The bacterium resistant to the antibiotic culture fluid from *Corticium abeuns* was as susceptible to penicillin as the normal strain of *Staph. aureus* and nearly as susceptible to streptothricin as the normal strain.

Whether any of the fungi included in this survey are possible sources of important antibiotic materials must be determined by further investigation.

#### SUMMARY

The antibacterial activity of over 400 fungi including over 300 wood-destroying organisms and 22 dermatophytes against *Staphylococcus aureus* and *Escherichia coli* was surveyed. Somewhat over 200 of the fungi exhibited antibacterial activity. For a considerable proportion the inhibition of bacterial growth did not appear to be caused by hydrogen-ion concentration developed by the fungus. None was as effective as *Penicillium notatum* in producing material active against *Staph. aureus*, and although some inhibited *E. coli* none affected the latter organism as much as it affected *Staph. aureus*. Culture liquids active against *Staph. aureus* at a dilution of 1 to 1000 were obtained from *Pleurotus griseus* and *Irpex mollis*.

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AND

DIVISION OF FOREST PATHOLOGY, BUREAU OF PLANT INDUSTRY,

SOILS AND AGRICULTURAL ENGINEERING,

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BELTSVILLE, MARYLAND

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## STUDIES IN THE SAPOTACEAE—I. THE NORTH AMERICAN SPECIES OF CHRYSOPHYLLUM

ARTHUR CRONQUIST

For the purpose of this series of papers, North America is taken to include Mexico, Central America, and the West Indies, exclusive of Trinidad and Tobago. The work is done under the auspices of the Chicle Development Co., under the direction of Mr. B. A. Krukoff. I extend my thanks to them and to the curators of the following herbaria (designated hereinafter by the letters at the left), who have kindly loaned specimens for study:

A, Arnold Arboretum, Harvard University, Jamaica Plain, Massachusetts.

CR, Museo Nacional de Costa Rica, San José.

F, Chicago Natural History Museum, Chicago, Illinois.

G, Gray Herbarium, Harvard University, Cambridge, Massachusetts.

Mich, University of Michigan, Ann Arbor, Michigan.

MO, Missouri Botanical Garden, St. Louis, Missouri.

NY, New York Botanical Garden, New York.

PR, Tropical Forest Herbarium, U. S. Forest Service, Rio Piedras, Puerto Rico.

US, United States National Herbarium, Washington, D. C.

Y, Yale University School of Forestry, New Haven, Connecticut.

Since it is at present impossible to verify many of the older names, current interpretations of their application are accepted. No attempt is made to give full synonymy for the period before 1900. This can generally be found elsewhere, as in Pierre and Urban's treatment of the Sapotaceae of the West Indies (*Symb. Ant.* 5: 95-176. 1904).

In North America, at least, the genus *Chrysophyllum* is sufficiently well characterized and sharply enough separated from the other genera of the family so that it becomes feasible to treat it separately. The following generic description is intended only for North American plants, although it will of course apply in large part to the genus as a whole.

CHRYSOPHYLLUM L. Sp. Pl. 192. 1753

Shrubs or small to medium-sized trees with alternate exstipulate leaves; secondary lateral veins generally nearly parallel to the primary ones, the areolae with the long axis about parallel to the primary veins; flowers few to numerous in axillary clusters, occasionally solitary; sepals 5, occasionally 4 or 6, joined only at the base, not over 3 mm. long; corolla not over 6 mm. long, cylindrical or campanulate, with 5 (occasionally 4 or 6) lobes; stamens

as many as the corolla-lobes and opposite them; filaments inserted at or near the level of the sinuses, often connected by a slightly thickened ring in the corolla-throat; anthers extrorse, but the valves often so twisted as to open subintrorsely; staminodia absent, or occasionally 1 or more irregularly developed in the sinuses, in individual flowers; ovary about 4-12-celled, bearing a short columnar style and a single capitate more or less lobed stigma; ovules solitary in the locules, attached laterally or basilaterally, in flower; fruit fleshy, with one or sometimes several seeds; seed-scar large, broadly elliptic to subcordate, generally at least 5 mm. long, lateral or basilateral; endosperm copious.

Type species: *Chrysophyllum cainito* L.

#### KEY TO THE SPECIES

1. Leaves loosely spreading-hirsutulous beneath, the hairs strongly rufous when young, later sometimes fading, and perhaps eventually deciduous; calyx 2-3 mm. long;<sup>1</sup> immature fruit ellipsoid, over 2.5 cm. long; Costa Rica. 8. *C. hirsutum*.
1. Leaves from permanently rufous-tomentose to finely white-sericeous or strigose and glabrate beneath, but not loosely hirsutulous; calyx various, sometimes but not often over 2 mm. long; fruit various.
  2. Leaves densely and permanently rufous-tomentose or villous beneath, sometimes becoming paler in age.
    3. Stigma-lobes mostly 7-12; fruit several-seeded, 3 cm. thick or more, generally subglobose; general distribution . . . . . 6. *C. cainito*.
    3. Stigma-lobes mostly 5, rarely 4 or 6; fruit 1-seeded, much less than 3 cm. thick, subglobose or more commonly ellipsoid.
      4. Fruit subglobose, less than 1 cm. thick; leaves more or less obovate-elliptic, broadest above the middle, obtuse at the apex; Cuba . . . . . 9. *C. claraense*.
      4. Fruit ellipsoid, much longer than thick; leaves variously elliptic to ovate or lanceolate, or rarely obovate, generally broadest at or below the middle, often but not always pointed at the tip.
        5. Flowers appearing on old defoliated branches at the time new leaves are appearing elsewhere; fruit about 3 cm. long and 2 cm. thick; Tepic, Mexico . . . . . 7. *C. tepicense*.
        5. Flowers generally appearing in the axils of leaves; fruit not over 2.5 cm. long, about 1 cm. thick or less.
          6. Leaves narrowly elliptic or elliptic-lanceolate, acuminate at both ends; Haiti and the Dominican Republic . . . 12. *C. angustifolium*.
          6. Leaves evidently broader, generally rounded to acutish at the base.
            7. Corolla 3.1-5.0 mm. long, the lobes distinctly shorter than the tube, as measured from the inside, generally not at all auriculate; filaments inserted about at the level of the sinuses, connected by a slightly thickened ring in the corolla-throat; Greater Antilles, Bahama Islands, and Florida . . . . . 10. *C. oliviforme*.

<sup>1</sup> Measurements of the calyx are taken from the inside, where it is sharply differentiated from the receptacle.

7. Corolla 2.2–3.5 mm. long, the lobes equaling or generally a little exceeding the tube, as measured from the inside, commonly slightly auriculate; filaments generally inserted on the corolla-lobes, a little above the level of the sinuses, the thickened ring absent or obscure; Tamaulipas and San Luis Potosi, Mexico, to Honduras and El Salvador ..... 11. *C. mexicanum*.

2. Leaves finely appressed-villosulous or strigulose beneath, with usually white hairs, when young, sooner or later glabrate (sometimes more densely hairy and somewhat rufous in *C. bicolor*, but still glabrate).

3. Creases for the corolla-lobes showing plainly on the outside for about the same length as the free part of the lobes, because the lobes are joined within by a thin cylinder of tissue; calyx 1.0–1.5 mm. long; fruit only slightly if at all longer than thick, usually several-seeded; Panama and Costa Rica ..... 4. *C. panamense*.

3. Creases for the corolla-lobes extending only slightly if at all beyond the free part of the lobes; calyx often more than 1.5 mm. long; fruit various, often much longer than wide, generally single-seeded except in *C. bicolor*.

4. Filament-traces, or some of them, evident.

5. Corolla finely sericeous to near the base, the hairs white or somewhat yellowish, not rufous; stigma-lobes 5 or often more, sometimes as many as 9; fruit rounded at the end, not tapering to the style; general throughout the West Indies ..... 1. *C. argenteum*.

5. Corolla sparsely or moderately rufous-hairy above the middle, the hairs much coarser than in *C. argenteum*, generally confined to 5 patches, one on the lower part of each lobe and extending to the upper part of the tube; stigma-lobes 5; fruit generally tapering to the style; Puerto Rico and the Virgin Islands ..... 2. *C. pauciflorum*.

4. Filament-traces obscure.

5. Fruit nearly globose, about 1.5–2.0 cm. thick; stigma-lobes usually but not always more than 5; pubescence of the pedicels strongly rufous; Puerto Rico and the Virgin Islands ..... 5. *C. bicolor*.

5. Fruit ellipsoid, about 1 cm. thick or less; stigma-lobes 5, or occasionally 4 or 6; pubescence of the pedicels more or less grayish, or absent; Mexico and Central America.

6. Corolla more or less hairy on the outside, about 3.0–4.0 mm. long; Costa Rica ..... 3. *C. brenesii*.

6. Corolla glabrous, 2.2–3.5 mm. long; Mexico to Honduras. .... 11. *C. mexicanum*.

# 1. CHRYSOPHYLLUM ARGENTEUM Jacq. Enum. Pl. Carib. 15. 1760.

*C. glabrum* Jacq. Enum. Pl. Carib. 15. 1760.

*C. caeruleum* Jacq. Stirp. Select. Am. 52. ca. 1780.

*C. argenteum* var. *sphaerocarpum* Urb. Symb. Ant. 9: 417. 1925.

Commonly a small tree, sometimes larger and as much as 30 m. high, or sometimes a mere large shrub 3–4 m. high; leaves glabrous above, thinly sericeous or strigulose with whitish hairs beneath, sooner or later glabrate, commonly elliptic or oblong-elliptic, broadest near the middle, but carrying the width well toward both ends, sometimes more ovate, of various sizes up to about 20 cm. long and 8 cm. wide, rounded to acutish or abruptly acuminate.

nate at the apex, the very tip blunt; flowers generally several or numerous in a cluster, sometimes only a few, the pedicels mostly 4–13 mm. long; calyx about 1.5–2.5 mm. long, the sepals broad, rounded, more or less sericeous outside, with fine light-colored or slightly reddish hairs, sometimes also slightly hairy inside, the margins usually thin and smooth; corolla white to greenish or yellow, 4–6 mm. long, sericeous to near the base with fine white or somewhat yellowish hairs, the tips and margins of the lobes smooth, the lobes generally about half as long as the tube, or a little less, broadly rounded; filament-traces more or less conspicuous, or sometimes some of them obscure; anthers 0.4–0.8 mm. long; stigma 5–9 lobed, the lobes evident to obscure; fruit 1-seeded, dark red or purple to blue or nearly black, commonly ellipsoid, often rather broadly so, about 1.5–2 cm. long, varying to subglobose and only 1 cm. long; seed-scar basilateral, commonly extending to near the middle.

TYPE: None given; from Martinique, according to Index Kewensis.

DISTRIBUTION: Forests; general throughout the West Indies from Oriente, Cuba, to Trinidad; apparently not on the mainland; reported by collectors to vary from fairly common to rare.

LOCAL NAMES: caimitillo, petit caymite, carabam, lechesillo, caimito verde, bois-rabi, kaimitier-bois, bois de bouis, acomat, bois-glu, bois-bouis, petit bois, petit bouis, buit, buis, bris, buie, wild star apple.

CUBA: Crosby & Matthews s.n. (Y); Eggers 4759 (NY); Leon 11780 (US); Matanzas: Rugel 627 (G); Oriente: Ekman 4076 (US); Ekman 4142 (NY); Ekman 7376 (NY); Shafer 4419 (NY); Shafer 7709 (G, NY); Shafer 8815 (G, NY, US); Wright 345 (G, NY); Wright 1328 (G, MO); Wright 1636 (G, MO, NY). HAITI: Ekman 1464 (US); Ekman 2344 (US); Ekman 2387 (US); Leonard 5291 (NY, US); Leonard 8675 (G, NY, US); Leonard & Leonard 12423 (G, US); Leonard & Leonard 12445 (MO, US); Leonard & Leonard 12945 (A, NY, US); Leonard & Leonard 14519 (Mich, US); Nash 192 (NY); Nash 465 (NY); Nash 606 (NY); Nash & Taylor 1205 (NY). DOMINICAN REPUBLIC: Abbot 1526 (G, US); Abbot 1604 (G, US); Abbot 2159 (G, US); Eggers 2433 (A, NY, US); Ekman 15757 (US); Ekman 16442 (US); Fuertes 446 (A, G, MO, NY, US); Taylor 189 (NY); Taylor 299 (NY); Rose, Fitch & Russell 4332 (NY, US); Wright, Parry & Brummel 202 (US). PUERTO RICO: Britton & Britton 7201 (NY); Britton & Britton 7422 (NY, US); Britton & Britton 9980 (NY); Britton, Britton & Brown 6205 (NY); Britton, Cowell & Brown 4531 (NY); Britton, Cowell & Brown 5588 (G, MO, NY, US); Britton & Marble 955 (NY, US); Eggers 420 (G); Eggers 614 (NY); Eggers s.n. (June 1887) (US); Gregory 52 (NY, PR); Heller 6431 (NY, US); Hioram s.n. (May, 1914) (NY, US); Holdridge 396 (PR); Johnston 579 (NY); Otero 699 (NY); Otero 702 (NY); Shafer 3538 (NY, US); Sintenis 1162 (US); Sintenis 1465 (G, NY, US); Sintenis 1937 (MO, NY, US); Sintenis 4090 (US); Sintenis 4130 (G, NY, US); Sintenis 6205 (US); Sintenis 6234 (US); Stevenson 6310 (US); Underwood & Griggs 886 (NY, US); Wyddler 317 (F). ST. THOMAS: Britton & Marble 1323 (NY, US); Eggers s.n. (Sept. 22, 1876) (MO). TORTOLA: Britton & Shafer 824 (NY, US); Fishlock 478 (NY, US). SABA: Boldingh 2115 (NY). ANTIGUA: Box 861 (A, US); Box 1053 (US); Box 1346 (US). GUADELOUPE: Bertero s.n. (MO); Duss 2911 (3906) (NY, MO, F, G, A); Duss 2912 (F, G, MO, US, NY); Questel 1674 (US); Questel 2264 (US); Stehle 478 (US, Mich); Stehle 997 (NY). DOMINICA: Cooper 181 (G, NY, US); Hodge 1955 (G); Hodge 3368 (G); Ramage s.n. (August 23, 1888) (NY); Ramage s.n. (Feb. 4, 1889) (G). MARTINIQUE: Duss 263 (NY); Duss 265 (= 266, 269) (A, F, G, MO, NY, US); Duss 747 (NY); Hahn 717 (= 641) (NY); Hahn s.n. (July, 1869) (G, US); Sieber 71 (MO); Stehle 999 (NY); Stehle 2345 (NY); Stehle 5188 (US). ST. VINCENT: Eggers 6584 (A); H. H. & G. W. Smith 912 (G); H. H. & G. W. Smith 1283 (NY); H. H. & G. W. Smith 1756 (G); H. H. & G. W. Smith s.n. (Sept. 1889) (NY). GRENADA: Broadway s.n. (Feb. 14, 1906) (F, G); Eggers 6152 (A, US); Eggers 6474 (A, US).



## 2. CHRYSOPHYLLUM PAUCIFLORUM Lam. Tab. Encyc. 2: 44. 1793.

*C. pauciflorum* var. *nervosum* Pierre, Symb. Ant. 5: 159. 1904.*C. pauciflorum* var. *krugii* Pierre, l. c.

Tree mostly 4–20 m. high; leaves glabrous and shining above, thinly sericeous or strigulose beneath when young, soon glabrate, mostly lance-ovate or narrowly ovate and somewhat acuminate, sometimes more elliptic and merely acutish, of various sizes up to about 10 cm. long and 4 cm. wide, averaging much smaller than in *C. argenteum*; flowers mostly 1–5 in a cluster, the pedicels slender and often lax, about 3–10 mm. long, distinctly rufous-hairy; calyx about 1.3–2.0 mm. long, the lobes rufous-hairy, narrower than in *C. argenteum*, and, especially the outer, tending to be acutish, often becoming progressively shorter, broader, and more rounded in centripetal progression; corolla reported to be yellowish, about 3.5–5.0 mm. long, with a distinctly reddish-hairy patch near the base of each lobe and extending to the upper part of the tube, the patches rarely confluent on the tube, the hairs coarser and sparser than those of *C. argenteum*; corolla-lobes about 2/5–4/5 as long as the tube; filament-traces evident, or occasionally some of them obscure; anthers about 0.5–0.7 mm. long; stigma evidently 5-lobed; fruit 1-seeded, ellipsoid, generally rather narrowly so, somewhat tapering to the style and often also tapering to the base, commonly about 1.5 cm. long; seed more slender than in *C. argenteum*, tapering to each end; seed-scar basilateral, generally extending to about the middle.

TYPE: Lamarck cites no specimens, but refers to plate 38, figure 2, in Jacquin's *Stirp. Am. Leon.* 1760, and indicates Martinique as the habitat. The fruit shown there can scarcely be that of the plant currently called *C. pauciflorum*, but looks more like that of *C. argenteum*. The flowers are shown as solitary in the axils, however, as in *C. pauciflorum*. The leaves shown in the figure might belong to either species. Since the drawing shows flowers and mature fruit on the same twig, it seems not unlikely that it was synthesized from two specimens, one of each species. *C. pauciflorum*, as currently interpreted, does not occur on Martinique, but is restricted to Puerto Rico and the Virgin Islands. Alphonse De Candolle, in his treatment of *C. pauciflorum* in the *Prodromus* (8: 158. 1844.) indicates that he has seen a specimen from St. Thomas in the herbarium of the Museum of Paris. It seems probable that this specimen was available to Lamarck, and should be taken as the type, with the reference to the Jacquin drawing excluded. It is perhaps noteworthy that the specimen on which De Candolle's description was based had young fruit, but no mature fruit.

DISTRIBUTION: Wooded places; Puerto Rico and the Virgin Islands.

LOCAL NAME: Caimito de perro.

PUERTO RICO: Britton & Britton 8847 (NY); Britton & Britton 9306 (NY); Britton & Britton 9470 (NY); Britton & Britton 9800 (NY); Britton & Britton 9912 (NY); Britton, Britton & Brown 5903 (NY, US); Britton & Cowell 1328 (NY, US); Britton & Marble 2246 (NY, MO, US); Cook K.91 (NY); Shafer 2532 (NY, US); Sittenis 1991 (G, MO, NY); Stevens & Hess 4001 (NY); Underwood & Griggs 574 (NY, US). ST. THOMAS: Oersted 12344 (F); Britton & Britton 244 (G, NY, US); Britton & Marble 1373 (NY, US); Eggers 23 (G); Shafer & Fitch 1471 (NY, US). ST. JAN: Britton & Shafer 206 (NY, US). ST. CROIX: Britton, Britton & Kemp 148 (NY); Ricksecker 180 (MO, US); Thompson 431 (NY).

### 3. *Chrysophyllum brenesii* Cronquist, sp. nov.

Tree reported to be 5–10 m. high; leaves thinly white-sericeous or strigulose on both sides when young, soon glabrate and shining above, more tardily glabrate and dull beneath, elliptic, acuminate at both ends, or the base merely acute, up to 10 cm. long and 4 cm. wide; flowers several or fairly numerous in each cluster, the pedicels about 4–8 mm. long, provided with a thin covering of fine and appressed grayish hairs; calyx about 1.4–1.7 mm. long, the sepals appressed-hairy with gray hairs outside, and somewhat ciliolate on the margins, the outer sometimes also somewhat hairy within, broadly ovate and tending to be obtuse or acutish, the inner glabrous within, suborbicular and more rounded; corolla about 3–4 mm. long, with a hairy patch near the base of each lobe and extending to the top of the tube, the hairs often somewhat rufous; corolla-lobes about equaling the tube, or a little shorter; filament-traces obscure; anthers about 0.5–0.6 mm. long; stigma evidently 5-lobed; fruit (only one seen) apparently single-seeded, broadly ellipsoid or ellipsoid-obovate, 16 mm. long, 10 mm. thick, broadest a little above the middle, constricted at the apex to a short broad beak about 1.5 mm. long and 2.5 mm. thick.

Arbor 5–10 m. alta, foliis glabratiss ellipticis usque ad 10 cm. longis 4 cm. latis apicibus acuminatis basibus acuminatis vel acutis, floribus paucis vel subnumerosis pedicellis cinereis pilis appressis, corolla 3.0–4.0 mm. longa lobis tubo subaequilongis, antheris ca. 0.5–0.6 mm. longis, partibus adnatis filamentorum obscuris, drupis obovato-ellipticis 16 mm. longis 10 mm. crassis apicibus constrictis.

TYPE: *Brenes 4415*, hill of San Pedro de San Ramon, Alajuela, Costa Rica, 1025 m., September 3, 1925 (F); ISOTYPE (CR).

DISTRIBUTION: San José and Alajuela, Costa Rica, at 1000–1100 m.

COSTA RICA: *Brenes 4155* (CR); *Brenes 15623* (CR). San José: *Tondus 12718* (=Donnell-Smith Distr. 7443) (US, CR, G). Alajuela: *Brenes 5021* (F, CR); *Brenes 5446* (F, CR); *Quiros 972* (CR).

### 4. *CHRYSOPHYLLUM PANAMENSE* Pittier, Contr. U. S. Nat. Herb. 18: 165. 1916.

*C. panamense* var. *macrophyllum* Standley, Field Mus. Pub. Bot. 22: 366. 1940.

Tree about 6–15 m. high; leaves finely white-strigulose beneath when young, soon glabrate, elliptic or elliptic-obovate, broadest near or above the middle, commonly but not always cuneate or acutish at the base (less so when larger) and abruptly acuminate at the apex, of various sizes up to about 30 cm. long and 14 cm. wide, usually much smaller, but averaging larger than in other North American species; flowers numerous in axillary clusters, the pedicels about 3–7 mm. long, closely cinereous; calyx about 1.0–1.5 mm. long, but appearing longer from the outside because of the thickened receptacle, closely strigulose with grayish or slightly rufous hairs, the two outer sepals tending to be obtuse or acutish, the others broadly rounded; corolla pale green to yellowish or nearly white, about 4.1–5.2 mm. long, with a sparsely or moderately short-hairy patch near the base of each lobe and extending to the top of the tube, or the patches occasionally confluent on the tube; free part of the corolla-lobes only about 1.1–1.5 mm. long, about 1/4–2/5 as long

as the tube, but the creases showing clearly on the outside for about as long as the free part; anthers about 0.4–0.6 mm. long; filament-traces, or some of them, evident; stigma distinctly 5-lobed; fruit purple or reddish-purple, generally several-seeded, from oblate-spheroidal (pumpkin-shaped) to very broadly ellipsoid or ovate and pointed at the end, about 1–2.5 cm. long and 1.2–2.0 cm. thick; seed-scar basilateral, extending to the middle of the seed or beyond.

TYPE: *Pittier 4005*, Sirri River, Trinidad basin, Colon, Panama Canal Zone, near sea level, July 20, 1911 (G, US).

DISTRIBUTION: Panama Canal Zone to Costa Rica, chiefly on the Atlantic slope.

COSTA RICA: *Stork 1669* (F, Y). Cartago: *Tonduz 12852* (= Donn. Smith dist. #7572) (US). PANAMA: Bocas del Toro: *Cooper 353* (F, NY, Y); *Hart 150* (US). Cocle: *Williams 276* (NY, US). CANAL ZONE: Gatun: *Hayes s.n.* (Feb. 1, 1860) (A, F, G, MO, NY, US). Barro Colorado Island: *Ariles 969* (F); *Bailey & Bailey 397* (F); *Bangham 591* (A, F, US); *Salvoza 981* (A); *Shattuck 1024* (F); *Starry 82* (F); *Starry 118* (F); *Wetmore & Abbe 169* (A, F, G); *Zetek 3810* (F, MO); *Zetek 4327* (F); *Zetek 4328* (F); *Zetek 4330* (A, NY, F); *Kenoyer 494* (US).

The variety *macrophyllum* seems to me to consist merely of the larger-leaved specimens in herbaria, rather than representing a real entity.

In Costa Rica this species might be confused with *C. brenesii*, which has a narrower apparently single-seeded fruit, smaller and narrower leaves, and smaller flowers with obscure filament-traces, and lacks the thin layer of tissue that joins the lower half of the corolla-lobes in *C. panamense*.

##### 5. CHRYSOPHYLLUM BICOLOR Poir. Encyc. Suppl. 2: 15. 1811.

*C. eggersii* Pierre, Symb. Ant. 5: 155. 1904.

Small tree; leaves conspicuously reddish-sericeous beneath when young, later glabrate, the hairs sometimes fading before falling; leaves elliptic-ovate or elliptic, broadest near or below the middle, rounded to acutish at the base, acute to acuminate at the tip, up to about 13 cm. long and nearly 6 cm. wide; flowers several in each cluster, the pedicels 3–10 mm. long and closely or somewhat loosely rufous-hairy; calyx about 1.0–1.7 mm. long, the sepals broad, obtuse or rounded, closely rufous-hairy outside, and slightly so within, some of the inner ones commonly with smooth somewhat petaloid narrow margins; corolla thick and firm, about 3.5–4.7 mm. long, generally appearing relatively broader than in related species, the lobes (except for the margins) and upper part of the tube conspicuously rufous-hairy, more generally and evenly so than in *C. pauciflorum*; corolla-lobes shorter than the tube, at least as measured from the inside, sometimes equaling or slightly exceeding it as measured from the outside; filament-traces obscure; anthers about 0.6–0.8 mm. long; stigma about 5–9-lobed, the ovary with as many locules; fruit ovoid or subglobose, or reported to be sometimes pyriform, about 2–3 cm. long and 1.5–2 cm. thick, with one or occasionally several seeds; seeds relatively short and thick, the scar basilateral, extending to the middle or beyond.

TYPE: *Ledru*, Puerto Rico.

DISTRIBUTION: Puerto Rico and the Virgin Islands.

PUERTO RICO: *Stevenson 2151* (US). ST. THOMAS: *Britton & Britton 220* (NY); *Eggers s.n.* (July 18, 1876) (NY, G, MO); *Eggers s.n.* (July 21, 1876) (NY); *Eggers s.n.* (July 29, 1876) (G, MO). ST. CROIX: *Ricksecker 369* (G, MO, NY, US).

6. *CHRYSOPHYLLUM CAINITO* L. Sp. Pl. 192. 1753.

*C. cainito* var. *pomiferum* Pierre, Symb. Ant. 5: 154. 1904.

Small to medium-sized or large tree sometimes as much as 30 m. high; leaves soon glabrous, shining, and usually with evident slightly raised veins above, densely rufous-sericeous or -tomentulose beneath, sometimes becoming a little paler in age, elliptic or oblong, obtuse or acutish at the base, generally abruptly short-acuminate at the apex, up to about 16 cm. long and 8 cm. wide; flowers numerous in axillary clusters, the pedicels closely rufous-hairy, generally about 1 cm. long or a little more; calyx about 1.0–1.2 mm. long, closely rufescent, the lobes suborbicular; corolla greenish or yellowish, about 3–5 mm. long, the tube glabrous, the lobes rufous-hairy except near the margins, somewhat ovate, more tapering than in most species, equaling or usually a little exceeding the tube; anthers about 0.7–0.9 mm. long; filaments attached on the corolla-lobes near the base, their traces obscure; stigma discoid, about 7–12-lobed, the style very short, fruit yellow, green, or purple, large, 3 cm. or more thick, reported to reach or exceed 10 cm. thick, commonly subglobose, several-seeded; seeds flattened, obliquely obovate, with a broad essentially lateral scar extending nearly the length of the seed.

TYPE: Linnaeus cites no specimens, but refers to several other publications.

LOCAL NAMES: Star-apple, caimito.

DISTRIBUTION: Probably indigenous throughout the West Indies, where also cultivated; cultivated and naturalized throughout Central America and southern Mexico.

Citation of specimens seems superfluous.

7. *CHRYSOPHYLLUM TEPECENSE* Standley, Contr. U. S. Nat. Herb. 23: 1115. 1924.

"Branchlets brownish-tomentulose; leaves (very immature) on petioles 1.5 to 2 cm. long, the blades oblong-elliptic, 3.5–4 cm. long, 1.7–2 cm. wide, obtuse or rounded at base and apex, densely brown-tomentulose on both surfaces; flowers borne on defoliate nodes of old branchlets, numerous in each cluster, the pedicels 8 to 10 mm. long, puberulent; sepals 5, orbicular, 2 mm. long, minutely sericeous; corolla 3.5 mm. long, greenish, sparsely sericeous; fruit oval, about 3 cm. long and 2 cm. thick, 1-seeded; seed brown, smooth, about 2.2 cm. long, the hilum near the apex on the ventral side, 8 mm. long and 3.5 mm. wide." Description copied from the original; no specimens seen.

TYPE: *Rose 1456*, Acaponeta, Tepic, Mexico.

DISTRIBUTION: Known only from the type collection.

8. *Chrysophyllum hirsutum* Cronquist, sp. nov.

Shrub or small tree 3–7 m. high; leaves loosely rufous-hirsutulous on both sides when young, soon becoming glabrous, dark green, and shining above, more permanently hairy beneath, though perhaps eventually glabrate there too in old leaves, the hairs beneath a little shorter and stiffer than those above, sometimes fading a little in age; twigs of the season's growth loosely

rufous-hirsutulous; leaves elliptic, rounded to usually acuminate (sometimes abruptly so) at the apex, rounded to acute at the base, up to about 11 cm. long and 5.5 cm. wide; petioles less than 1 cm. long; flowers about 2–6 in each axillary cluster, the pedicels densely rufous-hairy, about 4–8 mm. long; calyx about 2.0–3.0 mm. long, densely and loosely rufescent, the lobes narrowly to broadly triangular-ovate, the outer ones generally hairy within near the margins and broader than the inner; corolla about 4.5–5.5 mm. long, rufous-hirsute with appressed hairs above the middle or to near the base; corolla-lobes nearly or quite half as long as the tube, as measured from the inside, a little longer outside; anthers about 0.8–1.0 mm. long; filament-traces obscure or sometimes visible; filaments connected by a slightly thickened ring in the corolla-throat; stigma 5-lobed, or, in 4-lobed corollas, 4-lobed; ovules attached laterally below the middle. in flower; immature fruit about 2.6 cm. long and 1.0 cm. thick, broadest about 1 cm. from the tip, apparently single-seeded.

*Frutex vel arbor parva, petiolis minus quam 1 cm. longis, foliis ellipticis plerumque acuminatis usque ad 11 cm. longis 5.5 cm. latis utrinque hirsutulis pilis rufis laxis patentibus, supra mox glabratis nitidis, infra pilis persistentibus vel tarde deciduis, pedicellis ca. 2–6. 4–8 mm. longis, calyce ca. 2.0–3.0 mm. longo dense et laxe hirsutulo pilis rufis, corolla ca. 4.5–5.5 mm. longa extra pubescente pilis appressis rufis, lobis dimidio tubo aequalibus, antheris ca. 0.8–1.0 mm. longis, stigmate 5-lobato, drupis (immaturis) anguste obovoideis 2.6 cm. longis 10 mm. crassis.*

TYPE: *Austin Smith 1776*, Villa Quesada, San Carlos, Alajuela, Costa Rica, 825 m., Caribbean rain forest zone, at edge of forest, March 14, 1939 (A); ISOTYPE (F).

DISTRIBUTION: Alajuela, Costa Rica.

COSTA RICA: Alajuela: *Austin Smith 1922* (A, F, MO); *Austin Smith P2593* (Kr, NY).

9. *CHRYSOPHYLLUM CLARAENSE* Urb. Rep. Sp. Nov. **21**: 68. 1925.

"*Frutex v. arbor parva. Rami terets cinerei, internodiis 0.5–1.5 mm. longis. Folia 4–6 mm. longe petiolata, obovata vel obovata-elliptica, inferne subsensim angustata, apice obtusiuscula v. obtusa, 2.5–4 cm. longa, 1–2 cm. lata, nervo medio per totam longitudinem impresso, lateralibus crebris supra vix conspicuis, subtus sub tomento absconditis, supra nitida ab initio glabra in sicco olivacea, subtus tomento ferrugineo posterius pallescente oblecta, coriacea. Flores non visi. Fructus (unicus tantum obvisus) 5 mm. longe pedicellatus, globulosus perpauculo longior quam crassus, 8 mm. longus, 7.5 mm. crassus.*" Description copied from the original; no specimens seen.

TYPE: *Ekman 18891*, "in Cuba prov. Santa Clara prope Casilda in fruticetis litoralibus solo araneose, m. Mart. fruct."

DISTRIBUTION: Known only from the type collection.

10. *CHRYSOPHYLLUM OLIVIFORME* L. Syst. ed. 10. **2**: 937. 1759.

Shrub or more commonly a small tree, sometimes as much as 20 m. high; leaves much like those of *C. cainito*, glabrous and shining above, densely rufous-sericeous or tomentulose beneath, or occasionally relatively pale beneath, elliptic or oblong to nearly ovate, obtuse to acute or more commonly

abruptly short-acuminate at the apex, averaging a little smaller than in *C. cainito*, seldom more than about 10 cm. long and 5 cm. wide (rarely to 14 cm.  $\times$  8 cm.), and with the veins less evident and scarcely raised on the upper surface; flowers numerous to few or even solitary in the axils, the pedicels closely rufous-hairy, mostly about 4–7 mm. long; corolla yellowish or greenish, about 3.1–5.0 mm. long, glabrous or occasionally the upper part of the tube rufous-hairy, the lobes distinctly shorter than the tube, as measured from the inside; filaments inserted at about the level of the sinuses, connected by a slightly thickened ring in the corolla-throat, the traces obscure or occasionally evident; anthers commonly 0.6–0.8 mm. long; stigma distinctly 5-lobed; fruit reported to be purple, ellipsoid, single-seeded, about 1–2 cm. long and up to half as thick, distinctly oblique toward the base, at least in herbarium specimens, because of the broad basilateral seed-scar, which does not extend to the middle of the fruit.

TYPE: None given.

DISTRIBUTION: Common in thickets and scrub forest; southern Florida, the Bahama Islands, and the Greater Antilles.

LOCAL NAMES: Satin leaf, teta de burra, caimitillo, saffron tree, caimitier maron.

1. Leaves usually over 5 cm. long, often but not always at least half as wide as long; flowers generally several or numerous in a cluster *C. oliviforme* var. *typicum*.

1. Leaves generally 5 cm. long or less, and less than half as long as wide, or if sometimes more than 5 cm. long, then not more than  $\frac{2}{3}$  as long as wide; flowers about 1–6 in a cluster *C. oliviforme* var. *picardae*.

#### 10A. CHRYSOPHYLLUM OLIVIFORME var. *typicum* Cronquist, var. nov.

*C. oliviforme* L. Syst. ed. 10, 2: 937. 1759, sens. strict.

*C. oliviforme* var. *pallascens* Urb. Symb. Ant. 5: 157. 1904.

*C. oliviforme* var. *platyphyllum* Urb. l. c.

*C. brachycalyx* Urb. Symb. Ant. 7: 327. 1912.

*C. pallascens* Urb. Rep. Sp. Nov. 13: 470. 1915.

*C. platyphyllum* Urb. Rep. Sp. Nov. 13: 470. 1915.

*C. gonavense* Urb. Ark. Bot. 22A(17): 74. 1929.

*C. miragoaneum* Urb. Arkiv. Bot. 22A(17): 75. 1929.

Characters as in the key. Range of the species.

UNITED STATES: Florida: *Bessey* 81 (A); *Bessey* 105 (A, MO); *Bessey* 114 (A, MO); *Britton* 383 (NY); *Chapman* s.n. (1875) (G, MO, US); *Cowles* 909 (US); *Curtiss* 1758 (A, G, MO, NY, US); *Duckett* 201 (A, NY, US); *Eyles* 8156 (G); *Fredholm* 5557 (G); *Garber* s.n. (US, G, MO); *J. A. Harris* C21272 (US); *A. H. Howell* 865 (US); *A. H. Howell* 1021 (US); *Killip* 32875 (A); *McFarlin* 3836 (Mich); *McFarlin* 9728 (NY); *Moldenke* 5604 (NY); *Muenschner & Muenschner* 14120 (NY); *Muenschner & Muenschner* 14182 (A); *Rehder* 890 (A); *Rhoads* 8314 (A); *Safford & Mosier* 40 (US); *Seibert* 1171 (A, MO); *Simpson* 387 (G, NY); *Small* 2117 (NY); *Small* 2183 (NY); *Small* 7673 (NY); *Small* 8760 (NY); *Small & Carter* 1236 (NY); *Small & Carter* 2648 (NY); *Small & Mosier* 5903 (NY); *Small & Mosier* 6026 (G, MO, NY); *Small, Mosier & Dewinkeler* 10964 (US); *Small, Mosier & Thompson* 5779 (NY); *Tidestrom* 4222 (MO); *Webber* 66 (MO). BAHAMAS: *Brace* 239 (F); *Brace* 6856 (NY); *Britton* 134 (NY); *Britton* 3266 (NY, MO, US); *Curtiss* 31 (A, G, MO, NY, US); *Eggers* 4468 (US); *Northrop & Northrop* 262 (A, F, G, NY); *Wilson* 7724 (NY, MO, G). CUBA: *Gill & Whitford* 41 (Y); *Gill & Whitford* 84 (Y); *Griffith* 37 (NY); *Griffith* 64 (NY); *Rehder* 1201 (A); *Wright* 344 (MO, G); *Wright* 1322 (G, NY, MO, US). Pinar del Rio: *Earle*

& Wilson 1631 (NY); Earle & Wilson 1633 (NY); Earle & Wilson 1634 (NY); Shafer 10470 (NY, MO, US); Van Hermann 855 (US); Wilson 1210 (NY, US); Wilson 9367 (NY); Wilson 11575 (NY, MO, US). Isla de Pinos: Palmer & Riley 1021 (NY, US); Rowlee 218 (NY). Habana: Baker & Wilson 282 (NY); Earle & Wilson 2395 (NY); Shafer 17 (NY); van Hermann 155 (NY); van Hermann 309 (MO); van Hermann 397 (NY, MO, US); van Hermann 468 (A, NY, MO, US); van Hermann 5059 (A, G, US); Wilson 1001 (NY, US); Wilson 1002 (NY); Wilson 1071 (NY, US); Wilson 1989 (NY); Wilson 3527 (NY); Wilson 9464 (G, NY). Matanzas: Britton, Britton & Shafer 547 (NY); Britton & Wilson 26 (NY); Britton & Wilson 253 (NY); Rugel 5a (NY); Rugel 774 (NY). Santa Clara: Combs 234 (F, G, MO, NY); Combs 361 (F, G, MO, NY); Hodge, Howard & Godfrey 4166 (G, MO, NY, US); Hunnewell 11503 (G); Jack 4257 (A); Jack 4629 (A, MO, US); Jack 5482 (A, US); Jack 5895 (A, US); Jack 7480 (A, US); Jack 8138 (A, US); Salvoza 561 (A); L. B. Smith & Hodgdon 3206 (F, G, Mich, MO, NY, US). Camaguey: Shafer 57 (NY, US); Shafer 2903 (NY, US). Oriente: Matthews & Crosby 30 (Y); Ekman 10228 (NY). JAMAICA: Fredholm 3290 (NY); Harris 5363 (A, NY, US); Harris 5562 (G); Harris 5909 (A); Harris 9955 (US); March 795 (G); March 1467 (NY). HAITI: Barbour 32 (Y); Ekman H1819 (US); Ekman H2277 (US); Ekman H2336 (US); Ekman H2388 (US); Ekman H5113 (US); Ekman H6512 (US); Ekman H8398 (US); Ekman 8648 (US); Eyerdam 237 (G, US); Eyerdam 295 (A, G, MO, NY, US); Eyerdam 331 (G, MO, US); Holdridge 1341 (US); Leonard 3357 (G, NY, US); Leonard 5163 (US); Leonard 7031 (G, NY, US); Leonard 7710 (G, NY, US); Leonard 8449 (NY, US); Leonard & Leonard 11148 (Mich, US); Leonard & Leonard 11273 (MO, US); Leonard & Leonard 11475 (A, US); Leonard & Leonard 11643 (G, NY, US); Leonard & Leonard 12663 (A, G, US); Leonard & Leonard 12735 (US); Leonard & Leonard 12935 (US); Leonard & Leonard 13573 (NY, MO, US); Leonard & Leonard 14859 (US); Miller 311 (US); Nash 727 (NY); Nash & Taylor 1308 (NY, US). DOMINICAN REPUBLIC: Jaeger 185 (US); Eggers 2446 (A, NY, US); Ekman 13113 (US); Ekman 15767 (US); Fuertes 65 (NY); Fuertes 858 (A, G, US); Fuertes 1057 (A, MO); Fuertes 1311 (A); Fuertes 3011 (G, MO, NY, US); Rose, Fitch & Russell 3794 (NY, US); Rose, Fitch & Russell 4182 (G, NY, US); Rose, Fitch & Russell 4349 (US); Scarff 11 (F); Taylor 168 (NY); Taylor 420 (NY); Turckheim 3608 (G, MO, NY, US); Wright, Parry & Brummel 201 (US); Wright, Parry & Brummel 203 (G). PUERTO RICO: Britton & Britton 7887 (NY); Britton & Britton 8005 (G, NY, US); Britton & Britton 8030 (G, NY, US); Gregory 344 (PR); Heller 4426 (A, G, MO, NY, US); Miller 1645 (US); Sargent 302 (US); Sargent 507 (US); Sintenis 685 (G, US); Sintenis 2641 (US); Underwood & Griggs 162 (G).

10B. *CHRYSOPHYLLUM OLIVIFORME* var. *picardae* (Urb.) Cronquist, comb. nov.

*C. picardae* Urb. Symb. Ant. 5: 158. 1904.

*C. brachystylum* Urb. Symb. Ant. 7: 327. 1912.

*C. heterochroum* Urb. Ark. Bot. 22A(17): 74. 1929.

Characters as in the key; leaves sometimes becoming narrowly obovate, with tapering cuneate base.

TYPE: *Picarda* 1198, "Hab. in Haiti prope Port-au-Prince, n. Mart. fruct."

DISTRIBUTION: Haiti and the Dominican Republic; apparently not common.

HAITI: Ekman H2183 (US); Ekman 6748 (US); Ekman H5077 (US).

The var. *picardae* is well marked by its small relatively narrow leaves and few flowers, but passes readily into the more usual forms of the species. It might be regarded as transitional between *C. oliviforme* and *C. angustifolium*, but the rather scanty material available does not indicate any intergradation with the latter.

It has been remarked by collectors that in Florida the phase of the species that grows in pine woods seems different from the hammock phase, having the pubescence of the lower side of the leaves much lighter-colored. No clear-cut segregation of the species as a whole on this basis seems feasible, at least in the herbarium.

11. *CHRYSOPHYLLUM MEXICANUM* Brand. ex Standley, Contr. U. S. Nat. Herb. **23**: 1114. 1924.

Large shrub or more commonly a small to medium-sized tree, mostly 2–15 m. high, occasionally as much as 25 m.; leaves elliptic or elliptic-oblong to sometimes elliptic-ovate, acutish or abruptly short-acuminate at the apex, up to about 14 cm. long and 5 cm. wide, glabrous and shining above, the lateral veins sometimes prominent and a little raised, sometimes not, closely and relatively finely sericeous-strigose beneath, the lateral veins showing clearly through the pubescence, the hairs varying from more or less rufous to pale, the lower leaf-surface averaging considerably paler than in *C. cainito* or *C. oliviforme*, but usually redder than in *C. argenteum*, sometimes nearly glabrate in age, or occasionally soon glabrate, the hairs then very fine and inconspicuous; flowers numerous in clusters axillary to a leaf or leaf scar, in the latter case inferior to a leafy and floriferous branch of the season; pedicels closely hairy to occasionally subglabrous, mostly 3–5 mm. long; flowers averaging distinctly smaller than in *C. oliviforme*; calyx about 0.8–1.6 mm. long; corolla reported to be greenish to white, about 2.2–3.5 mm. long, the lobes equaling or generally a little exceeding the tube, as measured from the inside, commonly slightly auriculate; filaments commonly inserted on the corolla-lobes a little above the level of the sinuses, the thickened ring absent or obscure; anthers mostly 0.4–0.6 mm. long, stigma distinctly 5-lobed; fruit reported to be yellow to brown or black, ellipsoid, single-seeded, about 1–2 cm. long and half as thick, oblique at the base, at least in herbarium specimens, because of the broad basilateral seed-scar.

TYPE: *Purpus* 7679, Zacuapan, Vera Cruz, Mexico, 900–1000 m., Sept. 1916 (A, MO, US).

DISTRIBUTION: Tamaulipas and San Luis Potosi, Mexico, to Honduras and El Salvador.

LOCAL NAMES: cainito, zapote cainito, canela, palo de canela, piste, chike, siciya, zayoyillo, guayabillo, guava de danto, damsel.

1. Leaves early glabrate, the hairs fine and relatively inconspicuous, not rufescent; pedicels sparsely strigose or subglabrous; Oaxaca *C. mexicanum* var. *politum*.

1. Leaves tardily or not at all glabrate, the hairs coarser and forming an evident silky covering, often more or less rufescent; pedicels more evidently hairy; general from Tamaulipas and San Luis Potosi, Mexico, to Honduras and El Salvador *C. mexicanum* var. *typicum*.

11A. *CHRYSOPHYLLUM MEXICANUM* var. **typicum** Cronquist, var. nov.

*C. mexicanum* Brand. ex Standley, Contr. U. S. Nat. Herb. **23**: 1114. 1924, sens. strict.

Characters as in the key. Range of the species.

MEXICO: *Karwinski* 4243 (NY—Photo); *Sessé, Mocino, Castillo & Maldonado* 5104 (F). Tamaulipas: *Palmer* 321 (NY, US). San Luis Potosi: *Edwards* 645 (F, MO). Vera Cruz: *Purpus* 8038 (G, MO, NY, US); *Purpus* 8258 (A, G, MO, NY, US); *Purpus* 8258a



(G, MO, NY, US); *Purpus* 10775 (A, MO, F, Mich, US); *Williams* 8643a (F). Oaxaca: *Liebmann* 308 (F, NY, US); *Liebmann* 12343 (F); *Reko* 3082 (US); *Reko* 3498 (US). Yucatan: *Gaumer* 896 (A, F, G, MO, NY, US); *Gaumer* 24272 (A, F, G, NY, MO); *Lundell* 1190 (A, F, G, Mich, MO, NY, US); *Lundell* 1246 (F, G, Mich, MO, NY, US); *Lundell & Lundell* 7561 (A); *Millspaugh* 1555 (F); *Steggerda* 40a (F); *Stewart* 257 (G). Quintana Roo: *Lundell & Lundell* 7639 (A). Chiapas: *Matuda* 2621 (A, F, Mich, NY); *Matuda* 4768 (A, MO, NY); *Purpus* 167 (US); *Purpus* 10167 (NY, US). GUATEMALA: El Peten: *Bartlett* 12276 (Mich, US); *Lundell* 3501 (Mich); *Mercedes* 396 (Mich, MO). Alta Verapaz: *Standley* 70149 (A, F). Izabal: *Standley* 23942 (US). Quezaltenango: *Skutch* 1333 (A, NY, F, US). BRITISH HONDURAS: *Castillo* 21 (F, Y); *Gentle* 10 (F); *Gentle* 149 (A, F, Mich, NY, US); *Gentle* 245 (F, Mich, US); *Gentle* 1821 (A, F, Mich, MO, NY); *Gentle* 2975 (A, F, Mich, NY, US); *Gentle* 3085 (NY, A, Mich); *Gentle* 4092 (A, MO); *Gentle* 4744 (NY); *Heyder* 32 (US, Y); *Karling* 53 (NY, A, US); *Kluge* 20 (Y, US); *Lundell* X11 (US); *Lundell* LP12 (F); *Lundell* 4744 (Mich, MO); *Lundell* 6415 (NY, Mich); *Meyer* 83 (F, Mich); *Schipp* 303 (A, F, G, Mich, MO, NY, US); *Schipp* 753 (A, F, G, Mich, MO, NY); *Winzerling* V-2 (F, US, Y). HONDURAS: Camayagua: *Standley* 56505 (A); *Yuncker, Dawson & Youse* 5730 (F, G, Mich, MO, NY). Tegucigalpa: *von Hagen & von Hagen* 1145 (NY). Yoro: *Edwards* 632 (A, F, US); *Standley* 55060 (A, US). ATLANTIDA: *Standley* 54747 (A, US); *Standley* 54751 (A, US); *Standley* 55179 (A, US); *Standley* 56868 (A, US). EL SALVADOR: *Calderon* 1088 (G, NY, US); *Calderon* 1393 (US). Ahuachapan: *Standley* 20048 (US).

11B. *CHRYSOPHYLLUM MEXICANUM* var. *politum* Cronquist, var. nov.

A var. typico differt foliis infra mox glabratis, pedicellis subglabris vel sparse strigosis.

TYPE: *Martinez-Calderon* 241, shrub in llanos, Chiltepec and vicinity, district of Tuxtepec, Oaxaca, Mexico, about 20 m.; July, 1940–February, 1941 (A).

DISTRIBUTION: Known only from the type collection, Oaxaca, Mexico.

The difference in pubescence between var. *politum* and the more usual forms of *C. mexicanum* is very pronounced, but seems not to be correlated with any other differences, so that it seems unlikely that the character is of more than varietal importance.

This species has sometimes been confused with its West Indian relative, *C. oliviforme*, from which it differs in its smaller flowers of somewhat different proportions and in the generally finer and lighter-colored pubescence of the lower side of the leaves, as well as several minor features such as the more abundant flower-clusters, often more numerous flowers, and the frequent occurrence of the flower clusters beneath lateral shoots. I have seen no evidence of intergradation, nor is there any range-overlap, and the two scarcely seem conspecific.

12. *CHRYSOPHYLLUM ANGUSTIFOLIUM* Lam. Tab. Encey. 2: 44. 1793.

*C. montanum* Urb. Rep. Sp. Nov. 3: 469. 1915.

Tree; leaves narrowly elliptic or elliptic-lanceolate, acuminate at both ends, mostly about 4–7 cm. long and 10–20 or 25 mm. wide, commonly 3–5 times as long as wide, the larger ones sometimes a little wider, green and shining above, but commonly with some inconspicuous cobwebby-villous white or slightly reddish hairs, at least until maturity, when often glabrate,

densely villous-tomentose with rufous hairs beneath, the veins more or less evident on the upper surface, and generally pointing more nearly forward than in other species, but highly variable in that respect, chiefly according to the relative width of the leaf; flowers few or solitary in axillary clusters, the strongly rufous hairy pedicels mostly 5–8 mm. long; calyx densely rufous-hairy, about 1.5–1.8 mm. long, the outer sepals tending to be deltoid-ovate and acute or acutish, the inner ones broad, rounded, and shorter; corolla about 4.4–4.9 mm. long, the lobes shorter than the tube, which generally has a few hairs on the outside near the sinuses; anthers about 0.5–0.8 mm. long, the thickened ring more or less evident or sometimes obscure; filament-traces obscure; stigma 5-lobed; fruit single-seeded, ellipsoid, similar in size and shape to that of *C. oliviforme*.

TYPE: None given, but stated to come from Santo Domingo. Possibly the Martin collection cited by Pierre and Urban.

DOMINICAN REPUBLIC: *Fuertes* 630 (NY, US); *Fuertes* 1296 (A, G, US).

DISTRIBUTION: Haiti and the Dominican Republic.

This apparently rare species is related to *C. oliviforme*.

THE NEW YORK BOTANICAL GARDEN

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## DESCRIPTIONS OF TROPICAL RUSTS—VII<sup>1</sup>

GEORGE B. CUMMINS

The Uredinales reported in this paper were collected, for the most part, by C. G. Hansford in Uganda and by F. C. Deighton in Gold Coast and Sierra Leone and were made available through the courtesy of Miss E. M. Wakefield and Dr. G. R. Bisby. Of the species from other regions, four were collected in Australia by Mrs. Clemens and one was intercepted in customs as from Venezuela. Type specimens are deposited in the Arthur Herbarium of the Purdue University Agricultural Experiment Station. African specimens are also in the herbaria of either the Royal Botanic Gardens or the Imperial Mycological Institute, Kew and the Australian collections are in the Queensland Herbarium, Botanic Gardens, Brisbane.

*PHAKOPSORA HANSFORDII* Cumml. On *Alcornua cordifolia*, UGANDA: Kawanda, June 1939, *Hansford 2474*; on *Acalypha* sp., UGANDA: Kigezi, Aug. 1937, *Hansford 2152*.

Pycnia, aecia, uredia, and telia are present in No. 2474. The telia are so closely associated with the aecial infections as to strongly indicate that all sori belong in the life cycle of the species. The aecial stage is as follows:

Pycnia amphigenous, or mainly epiphyllous, subcuticular, lenticular or usually applanate, 30–35  $\mu$  high, 65–110  $\mu$  wide, hymenium flat, paraphysate. Aecia amphigenous, occurring along the veins with accompanying hypertrophy involving lengths up to 1.5 cm. or in small scattered groups. Peridium nearly colorless, 165–190  $\mu$  in diameter and up to 1.0 mm. in length but fragile, lacerate, and usually broken at the host; peridial cells cuboid, rhomboid or oblong, 15–19  $\times$  20–30  $\mu$ , inner wall moderately verrucose, 2.5–3  $\mu$  thick, outer wall punctate-striate, 2.5–3  $\mu$  thick, cells abutted or slightly overlapping, aeciospores ellipsoid or oblong-ellipsoid, 15–18  $\times$  19–25  $\mu$ ; wall pale yellowish brown or nearly hyaline, 1–1.5  $\mu$  thick, finely verrucose.

If the aecia actually belong in the life cycle, *P. hansfordii* is the first species of *Phakopsora* known to have cupulate aecia. Mundkur (*Mycologia* **35**: 542, 1943) has reported uredinoid aecia, unaccompanied by pycnia, as occurring in *P. stereospermi* Mundkur. He describes the aecia as lacking peridia and paraphyses and as having catenulate, echinulate aeciospores. Examination of a portion of the type specimen, furnished by Dr. Mundkur, leads me to question his description. The sori appear to be ordinary uredia (*Uredo stereospermi* Syd., in fact) with pedicellate spores produced on well-developed, brown, sporogenous basal cells. The telia are crustose with the spores strictly catenulate. *P. stereospermi* is not a species of *Phakopsora*.

<sup>1</sup>Journal Paper Number 181, of the Purdue University Agricultural Experiment Station. Contribution from the Department of Botany and Plant Pathology. The sixth article of this series was published in Bull. Torrey Club **70**: 517–530, 1943.

*Phakopsora apoda* (Har. and Pat.) Mains. On *Pennisetum polystachyum*, UGANDA, Pallisa, Bugwere, Jan. 1930, *Hansford 1024*; on *Setaria aequalis*, UGANDA: Kampala, Feb. 1930, *Hansford 1059*.

Uredia and telia are present on the *Pennisetum* but only uredia on *Setaria*. The characteristics of the uredia indicate that the rust on these hosts is identical with or closely related to *P. apoda*. Mains (*Mycologia* **30**: 45. 1938) has published photographs of telia from the original collection made in French Congo. No other reports of the species have been published.

*Phakopsora grewiae* (Pat. and Har.) Cummins, comb. nov. (fig. 1) (*Uredo grewiae* Pat. and Har. Jour. de Bot. **14**: 237. 1900). On *Grewia* sp., Thies (Cayor), Senegal, *Chevalier*.

Telia amphigenous, scattered or in small groups, blackish brown, subepidermal in origin but becoming erumpent, pulvinate or short cylindric, round, 64–165  $\mu$  in diam., 100–140  $\mu$  high; teliospores without definite arrangement, varying in size and shape, the marginal spores usually cuboid or globoid, the central cells usually oblong, 8–14  $\times$  11–23  $\mu$ ; wall cinnamon- or chestnut-brown, darkest in the outer spores, 1.5–2  $\mu$  thick, the apex uniform or thickened to 3  $\mu$ , smooth.

This specimen, a part of the Patouillard herbarium and made available through the courtesy of Dr. D. H. Linder, was collected in the type locality (Thies). The species is a typical *Phakopsora* and differs from *Uredo corbiculoides*, described below, for reasons enumerated under that species.

*Phakopsora desmium* (Berk. & Br.) Cummins, comb. nov. (*Aecidium desmium* Berk. & Br. Jour. Linn. Soc. **14**: 95. 1875; *Uredo gossypii* Lagerh. Jour. Myc. **7**: 48. 1891; *Kuehneola gossypii* Arth. N. Am. Flora **7**: 187. 1912; *Uredo desmium* Petch Ann. Bot. Gard. Peradeniya **5**: 247. 1912; *Cerotelium gossypii* Arth. Bull. Torrey Club **44**: 510. 1917; *Kuehneola desmium* Butl. Fungi & Dis. Plants 363. 1918).

An examination of the specimen (on *Gossypium acuminatum*, Santiago, Cuba, Mar. 1903, *L. M. Underwood & F. S. Earle 159*) upon which Arthur (*l.c.*) based his description of telia and his transfer to the genus *Kuehneola* proves that the teliospores are not catenulate but lack special orientation. The telia are typically phakopsoroid.

*Angiopsora hansfordii* Cummins, sp. nov. Pycniis et aeciis ignotis. Uredii hypophyllis, subepidermalibus, sparsis vel laxe aggregatis, ovalis vel oblongis, 0.3–1.0 mm. longis, flavidis; paraphysibus peripherales incurvatis, hyalinis vel pallide flavidis, 9–15  $\times$  25–40  $\mu$ ; membrana 1–1.5  $\mu$  cr., ad apicem 2–5  $\mu$  cr.; urediosporae late ellipsoideae, ellipsoideae vel obovoideae, 14–19  $\times$  20–27  $\mu$ ; membrana pallide flavida, 1.5–2  $\mu$  cr., minuteque verrucoso-echinulata; poris germ. obscuris. Teliis inter urediis sparsis, castaneis, subepidermalibus, indehiscentibus, ovalis vel oblongis, 0.3–1.0 mm. longis; teliosporis plerumque 2 superpositis, cuboideis vel oblongis, 9–17  $\times$  18–30  $\mu$ ; membrana pallide castaneo-brunnea, 1.5  $\mu$  cr., ad apicem 2–5  $\mu$  cr., levi.

On *Melinis tenuissima*, UGANDA: Kyasoweri, Elgon, Dec. 1933, *Hansford 1714* (TYPE).

*Uredo melinidis* Kern, the only other rust described on the genus *Melinis*, has cinnamon-brown urediospores with equatorial pores and sori without paraphyses. No species of *Angiospora* has been reported from Africa previously.

CROSSOPSORA FICT Arth. & Cumm. On *Ficus capensis*, UGANDA: Mukono, Kiagwe, June 1942, *Hansford* 3051.

This species, previously known only from the type collected in Luzon on *Ficus variegatus*, is characteristic because of the cinnamon-brown, angularly obovoid urediospores having three pores located in the angles. Telia are not present in Hansford's specimen.

CROSSOPSORA ANTIDESMAE-DIOICAE (Racib.) Arth. and Cumm. On *Antidesma venosa*, UGANDA: Entebbe Road, June 1942, *Hansford* 3012.

The species has not been reported from Africa previously.

**Cerotelium deightonii** Cummins, sp. nov. Urediis hypophyllis, subepidermalibus, sparsis, flavidis, rotundatis, 165–250  $\mu$  diam.; peridio hyalino fragili hemisphaerico dein poro aperto einctis; urediosporae oblongae, obovoideae vel late ellipsoideae, 13–18  $\times$  20–30  $\mu$ ; membrana 1–1.5  $\mu$  cr., ad apicem usque ad 5  $\mu$  cr., aureo-brunnea, moderate echinulata; poris germ. 2. aequatorialibus. Teliis urediis similibus sed eperidiatis; teliosporis 6–10 catenatim superpositis, plerumque oblongis, 11–15  $\times$  13–24  $\mu$ ; membrana hyalina, 0.5–1  $\mu$  cr., levi; statim germinantis ad apicem in basidium typicum; basidiosporae globoideae, 7–9  $\mu$  diam.

On *Phyllanthus discoides*, SIERRA LEONE: Makene, January 27, 1939, *Deighton* 1772 (TYPE).

Pycnia and aecia, apparently *Accidium phyllanthi* P. Henn., in sufficiently intimate association to suggest relationship occur on the leaves with the uredia and telia. The subcuticular pycnia and cupulate aecia correspond in structure to those of *C. dicentrae* (Trel.) Mains and Anders. but lack the systemic habit of that species.

Pycnia abundant, subcuticular, hypophyllous, lenticular to applanate, 120–165  $\mu$  diam., hymenium flat, aparaphysate. Aecia on brown spots, in groups reaching a diameter of 1.3 mm., cupulate, yellowish, the margin recurved, 0.3–0.5 mm. diam., aeciospores globoid or broadly ellipsoid, 16–20  $\times$  20–25  $\mu$ ; wall 1–1.5  $\mu$  thick, hyaline or nearly so, verruculose.

UROMYCES LEPTODERMUS Syd. On *Brachiaria platynota*, UGANDA: Kawanda, July 1940, *Hansford* 2766; on *Panicum deustum*, UGANDA: Kawanda, Aug. 1940, *Hansford* 2772; on *Setaria pallide-fusca*, UGANDA: Kisoro and Kabale, Kigezi, Aug. 1937, *Hansford* 2192, 2228; on *Setaria rubiginosa*, UGANDA: Kampala, Jan. 1930, *Hansford* 1051; on *Setaria verticillata*, UGANDA: Kampala, Jan. 31, 1930, *Hansford* 1043, Kabale, Kigezi, Aug. 1937, *Hansford* 2230.

Teliospores are present in No. 1043 and agree in all respects with those of *U. leptodermus*. It is probable that all specimens cited above belong to this species.

**UROMYCES PRETORIENSIS** Doidge. On *Aneilema* sp., UGANDA: West Nile, June 1936, A. S. Thomas (Hansford No. 1994); on *Commelina vogelii*, GOLD COAST: Aburi, Sept. 2, 1937, Deighton CB960.

The urediospores described by Doidge are apparently amphispores since, in Deighton's collection, there also occur urediospores with a wall thickness of 1.5–2  $\mu$ . These spores occur in separate sori or occasionally in the sori which produce the thick-walled amphispores. The rust on *Aneilema* consists of amphisori and telia.

**UROMYCES SCHINZIANUS** P. Henn. (fig. 7). On *Bauhinia fassoglensis*, UGANDA: Bukwa, Elgon, Dec. 1933, Hansford 1699.

The Sydows (Ann. Myc. 6: 136. 1908) have reported that Hennings' description was based upon the *Uredo* form and that he incorrectly described the urediospores as being teliospores. The Sydows' description of the urediospores corresponds so closely to those in Hansford's specimen that I feel confident that the rusts are the same and, since telia are present, a complete description is given below.

Uredia amphigenous but mainly hypophyllous, scattered or loosely grouped, round, 0.2–0.4 mm. diam., subepidermal, more or less pulverulent, yellowish brown or darker; urediospores globoid or broadly ellipsoid, 25–28  $\times$  27–31  $\mu$  (Sydow: 20–29  $\times$  22–32  $\mu$ ); wall 3–3.5  $\mu$  thick at sides, nearly uniform or thickened apically to 5  $\mu$ , golden to nearly chestnut-brown, variably bilaminate, the outer layer more or less hygroscopic, subhyaline, often conspicuous in mature spores, moderately echinulate; pores 3–5, equatorial or sometimes slightly above, appearing scattered unless the spore is properly oriented. Telia like the uredia or slightly larger and deep chestnut-brown, pulverulent; teliospores ovate or ellipsoid, rounded at the base and rounded or narrowly rounded at the apex, 18–23  $\times$  23–31  $\mu$ ; wall chestnut-brown, 3–4  $\mu$  thick at sides, 5–10  $\mu$  at the apex which is usually paler, finely reticulate with meshes 0.5–1  $\mu$  diam.; pedicel hyaline, fragile, about equal to the spore in length but often broken near the spore.

**Uromyces aspiliicola** Cummins, sp. nov. (fig. 9). Pycniis et aeciis ignotis. Urediis hypophyllis, subepidermalibus, in maculis minutis brunneis sparsis, rotundatis, 0.1–0.3 mm. diam., pulverulentis; urediosporis obovatis vel triangularis, 18–23  $\mu$  latis, 19–23  $\mu$  altis; membrana 1–1.5  $\mu$  cr., pallide cinnamomeo-brunnea, minuteque echinulata; poris germ. 2, aequatorialibus vel plus minusve subaequatorialibus. Teliis urediis conformibus sed atro-brunneis; teliosporae globoideae, 25–29  $\times$  27–30  $\mu$ ; membrana 4–6  $\mu$  cr., supra poro germ. umbono subhyalino leniter incrassata, minuteque rugosa vel fere levibus; pedicello hyalino, fragili, sporam brevior.

On *Aspilia asperifolia*, UGANDA: Kabaroni, Elgon, Dec. 1923, Hansford 1723 (TYPE).

*Uromyces baccarinii* Syd. appears, from the description, to be a generally similar species but with verrucose teliospores having long, semipersistent pedicels.

**PUCCINIA ANDROPOGONICOLA** Har. and Pat. (fig. 3). On *Cymbopogon giganteus*, GOLD COAST: Accra Plains, Aug. 5, 1937, *Deighton CB854*; on *Cymbopogon* sp., UGANDA: Serere, Teso, Apr. 1933, *Hansford 1632*; on *Hyparrhenia rufa*, MAURITIUS: Riche terre, Sept. 6, 1939, *Wiehe 170*; on *Hyparrhenia* sp., UGANDA: Serere, Teso, Jan. 1933, *Hansford 1620*.

All specimens cited above have both uredia and telia and agree in essential features with *P. andropogonicola*, the type of which has been available for comparison. The species has larger teliospores with thicker apex than do most species on Andropogoneae. In the uredial stage it is perhaps not separable with accuracy from *P. nakanishikii* Diet. and *P. kaernbachii* (P. Henn.) Arth. *P. andropogonicola* was described from French Congo.

**PUCCINIA NAKANISHIKII** Diet. On *Cymbopogon excavatus*, UGANDA: Kinizi, Kigezi, Aug. 1937, *Hansford 2149*; on *Cymbopogon martini*, UGANDA: Kawanda, Mar. 1941, Nov. 1942, *Hansford 2988, 3101*; on *Cymbopogon* sp., UGANDA: Serere, Teso, Mar. 1933, *Hansford 1626*.

Telia are present on Hansford's No. 2988, the teliospores deep chestnut-brown with persistent, brown pedicels approximately equaling the spores in length. I have had for comparison two specimens, both on *C. confertiflorus*, one from Belgian Congo and one from Ceylon.

**PUCCINIA INCOMPLETA** Syd.? On *Andropogon dummeri*, UGANDA: Kawanda, Mar. 1941, *Hansford 2990*.

*P. incompleta* was described from India on *Ischaemum* and has been reported from Okinawa Island and Formosa by Hiratsuka. Sydow described the paraphyses as strongly incurved with the wall much thicker on the convex than on the concave side. Hansford's specimen agrees in this respect but has slightly larger spores,  $17-23 \times 25-30 \mu$  as against  $16-20 \times 20-26 \mu$ .

Sydow did not describe telia but reports the teliospores as "perpaucis tantum visi, 1-septatis, adhuc immaturis." The uredia in Hansford's specimen and those described by Sydow possess characteristics common in *Angiopsora* or *Phakopsora* and the rust may be found to belong in one of these genera. The genus *Angiopsora* had not been recognized when Sydow described *P. incompleta* and *Phakopsora* had not been reported as occurring on grasses. It should be noted that Sydow made no mention of pedicels on the teliospores.

**PUCCINIA PROPINQUA** Syd. On *Amphilophis insculpta*, UGANDA: Butiaba, 1933, *H. B. Johnston* (comm. *Hansford 2246*). This species has not been reported from Africa. It was described from India on *Andropogon* and differs from *P. ccsatii* Schroet. in having somewhat smaller urediospores.

**Puccinia kenmorensis** Cummins, sp. nov. (fig. 6). Pyeniis et aeciis ignotis. Urediis amphigenis, in maculis brunneis sparsis vel laxe aggregatis,





ovalis, usque ad 0.5 mm. longis, brunneis, pulverulentis; paraphysibus plerumque capitatis, rectis, incurvatis vel geniculatis,  $11-16 \times 50-75 \mu$ ; membrana pallide flavida vel aurea,  $2-3 \mu$  cr., ad apicem usque ad  $8 \mu$  cr.; urediosporae globoideae, late ellipsoideae vel ellipsoideae,  $19-23 \times 23-29 \mu$ ; membrana uniformiter  $2-2.5 \mu$  cr., obscure cinnamomeo- vel castaneo-brunnea, minuteque echinulata; poris germ. 6-8 sparsis. Teliis ignotis; teliosporae ellipsoideae vel late ellipsoideae, utrinque rotundatae, medio non vel vix constrictae,  $18-22 \times 23-30 \mu$ ; membrana  $2-2.5 \mu$  cr., castaneo- vel pallide castaneo-brunnea, levi; pedicello brevi, hyalino, fragili, haud raro oblique inserto.

On *Bothriochloa decipiens*, AUSTRALIA: Kenmore, near Brisbane, May 18, 1943, Clemens (TYPE); Imbil, Queensland, Dec. 26, 1943, Clemens.

The location of the germ pores in the teliospores is uncertain but the presence of pale areas in the wall indicate that the pore of the upper cell is apical while that of the lower is in the lower half of the cell. The pedicels of the teliospores are fragile and deciduous. The urediospores and teliospores are both approximately chestnut-brown.

The combination of characters exhibited by this rust distinguish it from species described as having paraphyses and echinulate urediospores with scattered pores. Perhaps *Puccinia andropogonis-micranthi* Diet. is the most similar species but it has larger teliospores with longer pedicels. The number and arrangement of the pores is not given in the description of *P. andropogonis-micranthi* Diet. and no specimen has been available for examination.

PUCCINIA CACAO McAlp. On *Hemarthria uncinata*, AUSTRALIA: Imbil, Queensland, Dec. 27, 1943, Clemens.

Teliospores, present in the uredia, agree in all respects with *P. cacao* as described and illustrated by McAlpine. Although paraphyses were not described for the uredia of *P. cacao* they are present in the Clemens' specimen and are like those described for *Uredo mira* Cum. (Bull. Torrey Club 70: 528. 1943) on *Manisuris altissima* from Argentina. While I have not seen type material of *P. cacao* I am confident that *U. mira* should be considered as a synonym.

***Puccinia paspalina*** Cummins, sp. nov. (fig. 10). Pyeniis et aeciis ignotis. Urediiis amphigenis vel epiphyllis vel in vaginis culmisque evolutis, ovalis vel

#### Explanation of figures 1-8

FIG. 1. Freehand, unstained section of a telium of *Phakopsora grevilleae*.  $\times 800$ . FIG. 2. Freehand, unstained section of an uredium of *Ravenelia maranguensis* showing spores, brown peripheral paraphyses and adjacent gelatinous material. (From Hansford 1737.)  $\times 170$ . FIG. 3. Teliospores of *Puccinia andropogonicola*. (From Hansford 1632.)  $\times 800$ . FIG. 4. Freehand, unstained section of a sorus of *Uredo corbiculoides*. The sori characteristically arise in the sunken areas of the leaf. (From type.)  $\times 170$ . FIG. 5. Teliospores of *Puccinia dolosoides*. (From type.)  $\times 800$ . FIG. 6. *Puccinia kenmorensis*; urediospore and teliospore. (From type.)  $\times 800$ . FIG. 7. Teliospores and one urediospore of *Uromyces schinzianus*. (From Hansford 1699.)  $\times 800$ . FIG. 8. Teliospores of *Puccinia kampalensis*. (From type.)  $\times 800$ .

oblongis, 0.3–0.8 mm. longis, sparsis, pulverulentis, brunneis; paraphysibus nullis; urediosporae ovatae, obovoideae, ellipsoideae, frequenter plus minusve angulatae,  $19-26 \times 25-35 \mu$ ; membrana  $1.5 \mu$  cr., cinnamomeo- vel pallide cinnamomeo-brunnea, subtiliter breviterque echinulata; poris germ. 3, aequatorialibus. Teliis urediis similibus sed tarde dehiscens; teliosporae clavatae, variables, ad apicem obtusae vel rotundatae, deorsum attenuatae, medio non vel vix constrictae,  $23-30 \times 38-46 \mu$ ; membrana  $1.5-3 \mu$  cr., ad apicem non vel vix incrassata, flavida vel pallide aureo-brunnea, levi; pedicello persistenti, flavidulo,  $6-10 \mu$  longo; mesosporis numerosis.

On *Paspalum orbiculare*, AUSTRALIA: Birkdale, near Brisbane, Apr. 19, 1943, *Clemens* (TYPE); Brisbane, Mar. 4, 1943, Apr. 26, 1943, *Clemens*; on *P. dilatatum*, Mt. Coot-tha, near Brisbane, Feb. 24, 1943, *Clemens*.

It is probable that *Uredo paspalina* Syd. represents the uredial stage of this species but I have not had authentic material for comparison. If this assumption is true the rust may be rather widely distributed in the islands of the Pacific.

The long-covered telia, the pale irregular teliospores, the presence of numerous mesospores, and the lack of a definitely thickened apical wall clearly distinguish *P. paspalina* from *P. substriata* and other species of *Puccinia* described on *Paspalum*. Telia, present only in the type specimen and scantily in it, were found with certainty only on the leaf sheaths.

**Puccinia dolosoides** Cummins, sp. nov. (fig. 5). Urediis hypophyllis, sparsis, ellipticis, 0.2–0.5 mm. longis, flavo-brunneis, epidermide rupta inconspicue; paraphysibus nullis; urediosporae ovatae vel late ellipsoideae,  $21-27 \times 27-33$  (–36)  $\mu$ ; membrana  $1.5 \mu$  cr., moderate echinulata, pallide cinnamomeo-brunnea; poris germ. 3 (vel 4) equatorialibus. Teliis hypophyllis, subepidermalibus, indehiscens, sparsis vel laxe aggregatis, atro-brunneis, oblongis, usque ad 0.7 mm. longis, 0.1 mm. latis; teliosporae plerumque clavatae, ad apicem late rotundatae vel obtusae, deorsum attenuatae, ad septum non vel leniter constrictae, (16–)  $18-23$  (–25)  $\times$   $34-43$  (–50)  $\mu$ ; membrana castaneo-brunnea,  $1-1.5 \mu$  cr. vel ad apicem  $2-4 \mu$  cr.; pedicello brunneolo, persistenti, brevi,  $6-10 \mu$  longo.

On *Paspalum commersonii*, SIERRA LEONE: Njala, Sept. 24, 1926, *F. C. Deighton* 32 (TYPE).

This rust is similar, because of the small covered telia, to *P. dolosa* Arth. and Fromme and to *P. chaetochloae* Arth. In *P. dolosa* both the urediospores and the teliospores are smaller and the urediospores are triangular. *P. chaetochloae* has somewhat larger, more angular, and thicker-walled urediospores. The teliospores in Deighton's specimen are more regularly clavate than in *P. dolosa* or *P. chaetochloae*.

**PUCCINIA SUBSTRIATA** Ellis and Barth.? On *Solanum anomalum*, SIERRA LEONE: between Wiema and Dia, Apr. 6, 1936, *Deighton* 999.

In gross appearance and microscopic characteristics the aecia in this collection agree well with American collections of *P. substriata* (*Aecidium*

*tubulosum*). Inoculation experiments, using African material, will be necessary to prove the relationship since no African rust has yet been seen on *Paspalum* which can unquestionably be assigned to *P. substriata*.

***Puccinia stenotaphri*** (Syd.) Cummins, comb. nov. (*Uredo stenotaphri* Syd., Ann. Myc. 7: 544. 1909.) Uredia amphigenous but frequently mainly epiphyllous, scattered or in small groups and then usually on small yellowish spots, elliptical or oblong and attaining 0.5 mm. in length, pulverulent, light cinnamon-brown; paraphyses peripheral, in moderate numbers, slightly incurved, cylindrical, 9–12 × 50–75  $\mu$ ; wall yellowish or nearly hyaline, 1.5–3  $\mu$  thick, the apex uniform or slightly thickened; urediospores broadly ellipsoid, ovoid or ellipsoid, (22–) 25–28 (–30) × (28–) 30–40 (–46)  $\mu$ ; wall 1.5  $\mu$  thick, light cinnamon or cinnamon-brown, moderately echinulate; pores 4 or 5, equatorial, distinct. Telia amphigenous or mainly hypophyllous, subepidermal, long-covered by the epidermis, blackish brown, scattered or in small groups, oblong, 75–110  $\mu$  wide and attaining a length of 1 mm.; teliospores somewhat variable but mainly clavate or oblong-clavate, the apex obtuse-rounded, slightly or not constricted at the septum, narrowed toward the pedicel, 19–26 × (37–) 44–60  $\mu$ ; wall chestnut-brown, 1.5  $\mu$  thick at sides, thickened apically to 2.5–4  $\mu$ , smooth; pedicel brownish, persistent, 6–12  $\mu$  long.

On *Stenotaphrum dimidiatum*, MAURITIUS: June 1913, Wicke 115.

The Sydows (*l.c.*) did not describe paraphyses in *Uredo stenotaphri* and I have not had the type specimen for study, but I assume that the above transfer is valid. *P. stenotaphri* is similar to *P. penniseti* Zimm., a species in which paraphyses were not described nor are they present in material which I have had for comparison.

**PUCCINIA SCLERIAE** (Pazschke) Arth. On *Scleria naumanniana*, SIERRA LEONE: Njala, Nov. 7, 1938, Deighton 1637.

Only uredia are present but they agree with those of *P. scleriae*.

***Puccinia kampalensis*** Cummins, sp. nov. (fig. 8). Pycniis et aeciis ignotis. Urediiis hypophyllis vel rarius epiphyllis, sparsis, rotundatis, 0.2–0.3 mm. diam., pulverulentis, cinnamomeis vel obscure cinnamomeis; urediosporae late ellipsoideae vel ellipsoideae, 17–21 × 22–26  $\mu$ ; membrana 1.5  $\mu$  cr., cinnamomeo-brunnea, moderate echinulata; poris germ. 2, aequatorialibus. Teliis urediis conformibus sed plus minusve pallidiore; teliosporae oblongae, apicem versus plerumque attenuatae, ad septum leniter constrictae, basim versus attenuatae, 12–17 (–19) × (40–) 48–65  $\mu$ ; membrana 1  $\mu$  cr., ad apicem 2–3  $\mu$  cr., pallide aureo-brunnea, levi; pedicello hyalino, usque 40  $\mu$  longo.

On *Wedelia oblonga*, UGANDA: Kampala, Feb. 1937, Hansford 1073 (TYPE). *P. kampalensis* is similar to *P. caracasana* Syd., known only from Venezuela, but differs in having only two germ pores in the urediospores.

**PUCCINIA MINUSSENSIS** Thüm., var. ***africana*** Cummins, var. nov. Pycnia nulla. Aecia hypophylla et caulicola, peridio destituta, poro centrali aperta, 0.3–0.5 mm. diam., per totam superficiem plus minusve aequaliter sparsa;

aeciosporae globoideae vel ellipsoideae,  $14-20 \times 18-26 \mu$ ; membrana  $1.5 \mu$  cr. verruculosa. Uredii hypophyllis, sparsis,  $0.1-0.3$  mm. diam., cinnamomeo-brunneis; urediosporae globoideae vel late ellipsoideae,  $18-20 \times 19-24$  ( $-26$ )  $\mu$ ; membrana  $1.5-2 \mu$  cr., echinulata; poris germ. plerumque 3, aequatorialibus vel 3-4 plus minusve sparsis. Teliis urediis conformibus sed castaneis; teliosporae ellipsoideae,  $22-28 \times 29-35 \mu$ ; membrana  $2-2.5 \mu$  cr., castaneo-brunnea, verrucosa; poro superiore apicali, inferiore infra medium loculum sito; pedicello hyalino, fragili.

On *Lactuca* sp., UGANDA: Lwasamaire, Ankole, Aug. 1937, *Hansford 2156*; Kabale, Kigezi, Aug. 1937, *Hansford 2211* (TYPE).

This variety differs from the typical *P. minussensis* in that pycnia are lacking, the aecia are smaller and the urediospores usually have three equatorial pores. Aecia and uredia are present in No. 2156, the uredia on separate leaves or scattered among the aecia, while uredia and telia are present in the type.

**Sphenospora mera** Cummins, sp. nov. Pycniis et aeciis ignotis. Uredii hypophyllis, subepidermalibus, sparsis, rotundatis, usque ad  $0.5$  mm. diam., cinnamomeo-brunneis; urediosporae ovoideae vel late ellipsoideae,  $17-22 \times 23-27 \mu$ ; membrana  $2-2.5 \mu$  cr., cinnamomeo- vel aureo-brunnea, moderate echinulata; poris germ. 3 vel 4, aequatorialibus. Teliis hypophyllis, subepidermalibus, epidermide rupta inconspicue, in greges  $1-2$  mm. diam. concentricae dispositis, ceraceis, aureo-brunneis, plus minusve pulvinatis; teliosporae longitudinaliter uniseptatae, ad septum non constrictae, oblongo-ellipsoideae,  $11-14 \times 20-26 \mu$ ; membrana hyalina,  $0.5 \mu$  cr.; pedicello persistenti,  $9-12 \times 30-45 \mu$ , hyalino.

On *Cynoches chlorochilon*, VENEZUELA: locality unknown; intercepted in customs at San Juan, Puerto Rico, Nov. 16, 1943, by *L. J. McConnell 8719* (TYPE). Type deposited in the Arthur Herbarium; the Mycological Collections of the U. S. Department of Agriculture; and the Pennsylvania State College Herbarium.

This is the second species of *Sphenospora* to be collected on the Orchidaceae.

**Ravenelia hansfordii** Cummins, sp. nov. Pycniis et aeciis ignotis. Uredii hypophyllis, subepidermalibus, sparsis, rotundatis, usque  $0.4$  mm. diam., fusco-brunneis; periphysibus copiosis, cylindraceutis vel plus minusve clavatis, plerumque 1-septatis, brunneis vel deorsum hyalinis,  $8-14 \times 50-65 \mu$ ; membrana  $1 \mu$  cr., ad apicem  $2-4 \mu$  cr.; urediosporae ellipsoideae vel oblongae,  $14-18 \times 28-38 \mu$ ; membrana  $1-1.5 \mu$  cr., aureo- vel pallide cinnamomeo-brunnea, minuteque echinulata; poris germ. 4 (vel 5), aequatorialibus vel plus minusve subaequatorialibus. Teliis amphigenis, subepidermalibus, sparsis, atro-brunneis; capitulis teliosporarum convexis, castaneo-brunneis,  $65-99 \mu$  diam., ex sporis  $5-7$  in omni directione compositis; sporis singulis unicellularibus,  $13-20 \mu$  diam., papillis verruciformibus  $6-10$  minutis  $0.5-1.5 \mu$  altis obsitis; membrana  $0.5-1 \mu$  cr., ad apicem  $4-6 \mu$  cr.; cystidiis numerosis, globosis, pendulis, eodem numero quo sporis singulis, in aqua facile diffuentibus; pedicello ex hyphis pluribus composito, deciduo.

On *Acacia* sp., UGANDA: Serere, Teso, Jan. 1933, *Hansford 1616* (TYPE).

*R. hansfordii* differs from species described previously on *Acacia* because of longer urediospores, the low wart-like markings on the teliospores and especially because of the usually septate, puccinioid paraphyses.

**RAVENELIA BOTTOMLEYAE** Doidge. On *Albizzia grandibracteata*, UGANDA: Kawanda, July 1939, *Hansford* 2524.

The aecial stage, not previously described, is abundant on Hansford's specimen. Pycnia amphigenous, lenticular, 150–175  $\mu$  diam., subcuticular in origin but extending downward between and partially displacing the epidermal cells, aparaphysate, hymenium flat. Aecia uredinoid, occurring as a more or less complete ring about the pycnia, 2–5 mm. diam., usually associated with the veins, reddish brown, more numerous on the upper leaf surface; aeciospores asymmetrical, ovate, obovate or ellipsoid with pores face-view, 22–25  $\times$  29–36  $\mu$ , mainly oblong with pores lateral, 16–20  $\times$  29–36  $\mu$ ; wall laminate, the inner wall golden-brown, 1.5  $\mu$  thick, the outer wall hyaline or yellowish, 2–6  $\mu$  thick, investing the spore as a simple band, appearing as a more or less complete envelop when pores are face-view but as a conspicuous apical and slight basal cap when pores are lateral, rather closely and strongly aculeate with conical spines, smooth on the pore-bearing sides; pores 2, equatorial.

Doidge's description gives the thickness but does not mention the character of the wall of the urediospores, which is similar in structure to that of the aeciospores.

**RAVENELIA LAEVIODES** Arth. and Cum. On *Indigofera* sp., UGANDA: Serere, Teso, Oct. 1932, *Hansford* 1601; Kiukizi, Kigezi, Aug. 1937, *Hansford* 2153.

This species was described from the Philippine Islands and has not been reported from other regions. Both uredia and telia are represented in Hansford's collection and agree morphologically with *R. laevioides*. In the type specimen the telia are caulicolous whereas they are foliicolous in the African material.

**Ravenelia maranguensis** (P. Henn.) Cummins, comb. nov. (fig. 2) (*Uredo maranguensis* P. Henn. in Engler, Die Pflanzenwelt Ost-Afrikas und der Nachbargebiete, Teil C, p. 51, 1895). Uredia hypophyllous, subepidermal, usually in compact groups 1–3 mm. diam. on yellowish spots, pulvinate, round, 0.3–0.7 mm. diam., cinnamon-brown or becoming darker, opening at first by a narrow aperture surrounded by paraphyses and an extensive adjacent, gelatinous, subepidermal layer which apparently produces the paraphyses and is in turn dissolved as the sorus develops; paraphyses mainly capitate or clavate-capitate, 14–26  $\mu$  diam., the wall golden to chestnut, 3–9  $\mu$  thick at the apex; urediospores broadly ellipsoid or ellipsoid, 16–18  $\times$  18–25  $\mu$ ; wall 1.5–2  $\mu$  thick, pale yellowish or nearly hyaline, rather finely and closely echinulate; germ pores 6–9, scattered. Telia amphigenous but mainly epiphyllous and opposite the uredia, blackish brown; teliospore-heads convex, 80–135 (–140)  $\mu$  diam., about 35  $\mu$  thick, chestnut brown, the marginal spores bearing 1–6, usually 1–3, subhyaline, papillate tubercles 1–4  $\mu$  high; indi-

vidual spores 2-celled except the marginal row, 13–23  $\mu$  diam.; wall 1.5–2  $\mu$  thick at sides, 4–6  $\mu$  at apex; cysts hyaline, appressed, equal in number to the marginal cells, swelling and bursting in water; pedicel hyaline, composed of many hyphae, easily broken.

On *Indigofera arrecta*, UGANDA: Kisoro, Kigezi, Aug. 1937, *Hansford 2197*; on *Indigofera* sp., UGANDA: Butandiga, Mt. Elgon, Aug. 1934, *Hansford 1737*.

Both uredia and telia are present in No. 1737, from which the above description is drawn. I have had for study a specimen, probably part of the original collection, of *Uredo maranguensis* on *Indigofera arrecta* collected by G. Volkens at Marangu, Kilimandscharo in 1894. The sori are older and the gelatinous layer less conspicuous but the rusts are unquestionably the same. Because of the characteristic structure of the uredia, *R. maranguensis* is readily distinguishable from other species on *Indigofera*.

SPHAEROPHRAGMIUM ACACIAE (Cooke) Magn. On *Albizzia lebbek*, GOLD COAST: Aburi Bot. Gard., July 27, 1937, *Deighton CB827*; RODRIGUIS ISLAND: Oct. 1938, *Wiehe DR12*; on *Albizzia procera*, GOLD COAST: Aburi Bot. Gard., July 27, 1937, *Deighton CB826*; on *Cassia* sp., UGANDA: Serere, Teso, Jan. 1933, *Hansford 1622*.

It was impossible to find differences, either in the uredia or the telia, between the rust on *Albizzia* and on *Cassia* and they are considered to represent a single species.

**Phragmopyxis leonensis** Cummins, sp. nov. (fig. 11). Pycniis et aeciis ignotis. Uredia hypophylla, sparsa vel in maculis brunneis usque 2.5 mm. diam. aggregata, rotundata usque 0.3 mm. diam., flavida, subcuticularia; periphysibus copiosis, hyalinis vel brunneis, cylindraceis, ad basim conjunctis et septatis, crasse tunicatis, fere solidis, 10–18  $\times$  42–85  $\mu$ ; urediosporae late ellipsoideae vel ellipsoideae, 13–16  $\times$  16–19  $\mu$ ; membrana 1–1.5  $\mu$  cr., hyalina vel subhyalina, minuteque echinulata, poris germ. obscuris, sparsis, plus minusve 8. Teliis urediis conformibus sed castaneis; teliosporae cylindraceae, utrinque rotundatae, ex cellulis 2–3, plerumque 3, compositis, 19–23  $\times$  (37–) 42–50 (–54)  $\mu$ ; membrana bilaminata, pariete interiore aureo-vel pallide castaneo-brunnea 2  $\mu$  cr., exteriori subhyalina usque 4  $\mu$  cr., valde tuberculato-aculeata, aculeae usque 3  $\mu$  lata, 5  $\mu$  alta; pedicello sporam aequante vel longiore, hyalino, persistenti. Statim germ.

On *Cassia sieberiana*, SIERRA LEONE: Njala, Nov. 30, 1934, *Deighton 660* (TYPE).

This unusual rust is probably best referred to the genus *Phragmopyxis*, although in certain features it approaches the genus *Mimema*, established by Jackson (*Mycologia* 23: 338, 1931) to accommodate a species (*M. holwayi* Jacks.) on *Cassia* from Bolivia. In *Mimema* the sori are subepidermal with peripheral paraphyses and the teliospores cylindric with a uniformly thin, nonlaminar wall and a long, nearly solid pedicel. The genus is strongly reminiscent of *Hamaspora*, as pointed out by Jackson.

In *Phragmomyxis* the sori, other than pycnia, are likewise subepidermal with peripheral, but less strongly developed, paraphyses. The teliospores are phragmidoid with a conspicuously laminate wall, the outer hyaline portion hygroscopic, and pedicels which are nearly solid near the spore but delicate and evanescent or strongly hygroscopic in the lower portion. There are three or four equatorial pores in each cell of the teliospore in *Phragmomyxis*. In *Mimema* pores are not obvious but the basidium is produced at the apex of the upper cell and just below the septum in the other cells.

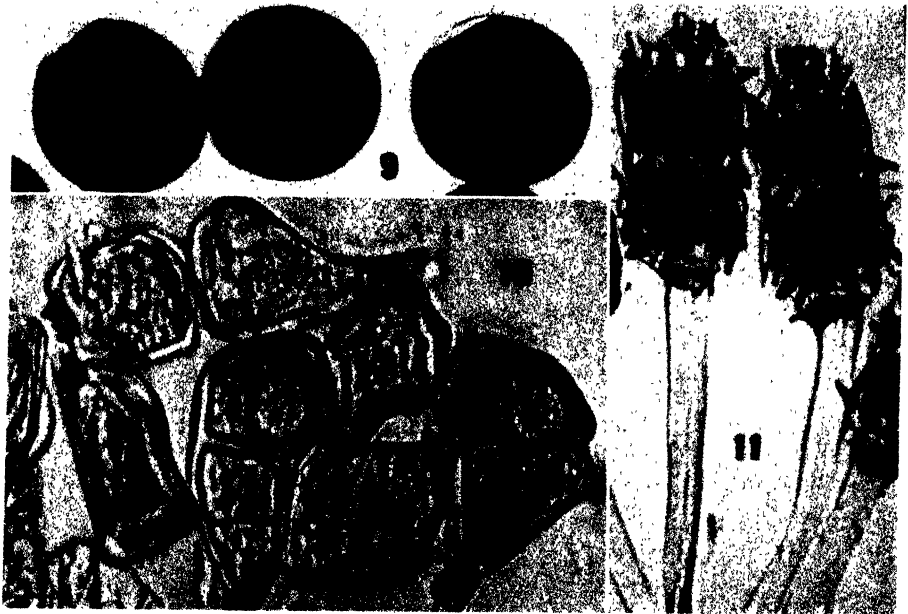


FIG. 9. Teliospores of *Uromyces aspidicola*. The wall is dark brown except for a slight hyaline umbo over the pore. (From type.)  $\times 800$ . FIG. 10. Teliospores of *Puccinia paspalua*. One-celled teliospores are common. (From type.)  $\times 800$ . FIG. 11. Teliospores of *Phragmomyxis leonensis*. (From type.)  $\times 800$ .

In Deighton's specimen the subcuticular position of the sori is not in conformity with either *Mimema* or *Phragmomyxis*. The large paraphyses are more like those in *Mimema*, but this is mainly a size similarity, and the urediospores offer no special features. The aculeate teliospores with their obviously laminate walls indicate relationship with *Phragmomyxis* but offer no similarity to *Mimema*. Germ pores have not been observed in Deighton's rust. There is, around the equator of each cell, a hyaline, smooth zone from which the basidium is produced but I have been unable to ascertain whether the basidium emerges from differentiated pores or whether the entire zone is equally susceptible to rupture during germination.

While recognizing that certain characteristics of this rust prevent unobjectionable assignment to any established genus, the number of characters in agreement with *Phragmopyxis* indicate that the species can be placed most logically in that genus.

**Pucciniosira deightonii** Cummins, sp. nov. Pycniis nullis. Teliis hypophyllis, in maculis brunneis usque 8 mm. diam. aggregatis, flavidis, aecidioideis, breviter cylindraceis; cellulis peridii plerumque oblongis,  $13-20 \times 24-44 \mu$ ; membrana  $3 \mu$  cr., minuteque verrucosa; teliosporis bicellularis plerumque ellipsoideis vel oblongo-ellipsoideis,  $(13-)$   $15-20$   $(-23) \times (19-)$   $22-29 \mu$ ; membrana  $1-1.5 \mu$  cr., pallide flavidula vel hyalina, minuteque verruculosa.

On *Jasminum pauciflorum*, SIERRA LEONE: Hill Station, May 25, 1935, *Deighton 717* (TYPE); Njala, May 19, 1934, *Deighton 654A*; Allen Town, Dec. 7, 1936, *Deighton 1133*.

The infections vary in that some cause somewhat corky, discoid hypertrophy while in others this is not obvious. Hypertrophy appears to be commonest in older infections in which the telia have largely disintegrated.

**Uredo arundinellae-nepalensis** Cummins, sp. nov. Urediiis amphigenis, in maculis brunneis aggregatis vel sparsis, ovalis vel oblongis, 0.2–0.6 mm. longis, brunneis, pulverulentis; periphysibus cylindraceis vel plus minusve incurvatis,  $9-12 \times 35-45 \mu$ , membrana hyalina vel flavidula,  $1-1.5 \mu$  cr., ad apicem usque  $6 \mu$  cr.; urediosporae ellipsoideae, ovoideae vel obovoideae,  $17-23 \times 25-33$   $(-39) \mu$ , membrana  $1-1.5 \mu$  cr., subtiliter echinulata, flavida vel aureo-brunnea; poris germ. inconspicuis, 4 vel 5, aequatorialibus.

On *Arundinella nepalensis*, AUSTRALIA: Lawnton, near Brisbane, Apr. 26, 1943, *Clemens*; Mt. Coot-tha, near Brisbane, February 24, 1943, *Clemens* (TYPE).

No rust previously reported on *Arundinella* is described as having paraphyses or urediospores with such thin walls. The paraphyses are usually thickened apically and dorsally and are similar, as are also the pale, thin-walled urediospores, to those of species of *Phakopsora* and *Angiopsora*.

**Uredo crassiperidiata** Cummins, sp. nov. Urediiis amphigenis, supepidermalibus, sparsis, fusco-brunneis, pulverulentis, ovalis, 0.2–0.35 mm. longis, poro centrali apertis, peridio crasso, ex cellulis elongatis brunneis composito, membrana  $2 \mu$  crassa; urediosporae variabiles ellipsoideae, oblongo-ellipsoideae, obovatae vel late ellipsoideae,  $18-23$   $(-26) \times (25-)$   $29-35$   $(-39) \mu$ ; membrana  $1.5-2 \mu$  cr., hyalina vel pallide flavida, tenuiter laxiusculeque echinulata ( $2-2.5 \mu$ ): poris germ. 3 vel 4 aequatorialibus parum conspicuis praeditis.

On *Scleria melanomphala*, SIERRA LEONE: Segbwema, Dec. 11, 1937, *Deighton 1482* (TYPE).

The peridium provides the principal distinguishing feature of this species. It is 3–8 cells in thickness in the basal portion and bears some resemblance to the subepidermal paraphyses found in certain loculate telia. The



peridial tissue extends beneath the sorus, where its upper layer becomes sporogenous. At the sides, and especially toward the apex, some of the cells of the inner layer extend inward as short, variable paraphyses. The urediospores are longer than those of other rusts of *Scleria*.

**Uredo achyranthicola** Cummins, sp. nov. Urediis plerumque epiphyllis, aggregatis vel sparsis, rotundatis, 0.2–0.4 (–0.7) mm. diam., pulverulentis, flavidis, epidermide rupta conspicue; urediosporae obovoideae, ellipsoideae vel late ellipsoideae, (13–) 15–18 × (19–) 21–26 (–29)  $\mu$ ; membrana 2–2.5  $\mu$  cr., moderate echinulata, pallide aurea vel flavida; poris germ. obscuris, verissimiliter plus minusve 6, sparsis.

On *Achyranthes aspera*, UGANDA: Kisoro, Kigezi, Aug. 1937, *Hansford 2194* (TYPE).

In 1937 Castellani and Ciferri (*Prodomus Mycofl. Afr. Orient. Ital.* p. 52) reported *Uredo achyranthis* P. Henn. on *Achyranthes aspera* although the Sydows (*Monogr. Ured.* 4: 591. 1924) state that Hennings' fungus is an *Albugo* and not a rust. Hansford's collection demonstrates that there is an *Uredo* on *Achyranthes* in Africa and, since Hennings' species is not a rust and since the *Uredo* differs from other rusts on *Amaranthaceae*, the above description is necessary.

**Uredo diocleae** Cummins, sp. nov. Urediis subepidermalibus hypophyllis, sparsis, pulverulentis, cinnamomeis, rotundatis, 100–175  $\mu$  diam.; urediosporae asymmetricae, globoideae vel late ellipsoideae, 19–23 × 22–26  $\mu$ , vel reniformae, 16–19 × 22–26  $\mu$ ; membrana 1.5  $\mu$  cr., cinnamomeo-brunnea, moderate echinulata; poris germ. 1 (vel 2?) plus minusve superaequatorialibus.

On *Dioclea reflexa*, SIERRA LEONE: Mamauka, Feb. 1, 1939, *Deighton 1815* (TYPE).

Asymmetrical urediospores are not uncommon in rusts parasitic on legumes but are especially characteristic of the genus *Sphacrophragmium*. Only one pore, located slightly above the equator in the concave side of the spore, was seen with certainty but it is possible that there are two. An area surrounding the pore and extending down the concave side to the hilem is smooth, while other portions of the wall are uniformly echinulate.

UREDIO FAMELICA Arth. and Cum. On *Mucuna urens*, SIERRA LEONE: Kenema, Dec. 5, 1937, *Deighton 1438*.

The spores in this collection average slightly smaller than those of the type, collected in Ecuador, but do not differ otherwise.

**Uredo corbiculoides** Cummins, sp. nov. (fig. 4). Urediis hypophyllis, subepidermalibus, in lacunae foliorum natis, sparsis vel laxe aggregatis, brunneis, plus minusve corbiculaeformibus; paraphysibus peripherales copiosis, incurvatis, brunneis, 6–13 × 50–100  $\mu$ , deorsum conjunctis, mem-

brana 1–2  $\mu$  cr., superne incrassato usque ad 4  $\mu$ ; urediosporae late ellipsoideae vel globoideae, 13–16  $\times$  16–20  $\mu$ ; membrana hyalina vel pallide aureo-brunnea, laxe breviterque echinulata; poris germ. obscuris.

On *Grewia* sp., UGANDA: Serere, Teso, Mar. 1933, *Hansford 1630* (TYPE).

This species has peculiar sori with abundant and conspicuous peripheral paraphyses which arise from an elongate, cellular, basal, stipe-like structure which arises from within the sunken areas which are characteristic of the leaves of the host. The spores are also produced from the apical layers of this cellular base and are sessile or nearly so. Their exact method of development was not ascertained.

*U. corbiculoides* differs from *Uredo grewiae* Pat. and Har. in having spores that are smaller (13–16  $\times$  16–20  $\mu$  as against 15–21  $\times$  20–28  $\mu$ ) and paraphyses that are twice as long (50–100  $\mu$  as against 25–45  $\mu$ ) as described for *U. grewiae*.

UREDOLONGAENSIS P. HEIM. ? On *Combretum* sp., GOLD COAST: Akwadum, Aug. 17, 1937, *Deighton CB908*; SIERRA LEONE: Mabang, Nov. 27, 1936, *Deighton 1346*.

It is questionable whether these collections are correctly referred to *U. longaensis* or whether they represent a related, but distinct, species. The sori are similar in habit, the spores are catenulate and of the same size but the wall is thickened apically in most spores, frequently to as much as 6  $\mu$ . The outermost layer of spores adheres to the epidermis in a peridium-like manner. These spores (or peridial cells?) are globoid, 13–16  $\mu$  in diameter and have walls of uniform thickness.

*Uredo pergulariae* Cummins, sp. nov. Uredii subepidermalibus, hypophyllis, sparsis vel laxe aggregatis, rotundatis, 0.3–1 mm. diam., pulverulentis, cinnamomeo-brunneis; urediosporae late ellipsoideae vel globoideae, 20–26  $\times$  23–29  $\mu$ ; membrana cinnamomeo-brunnea, 1.5–2.5  $\mu$  cr., moderate echinulata; poris germ. 4 (vel 3), aequatorialibus vel interdum plus minusve sparsis.

On *Pergularia* sp., UGANDA: Rife Range, Kiagwe, June 1942, *Hansford 3041* (TYPE).

*Uredo perscita* Cummins, sp. nov. Uredii hypophyllis, subepidermalibus, sparsis vel laxe aggregatis, pulverulentis, flavo-brunneis, rotundatis, 0.2–0.4 mm. diam.; paraphysibus peripherales copiosis, plerumque 1-septatis, incurvatis, inferne conjunctis, 13–21  $\mu$  latis et usque 80  $\mu$  longis, flavidis vel plerumque brunneis, deorsum pallidiores, membrano ubique 1.5–2.5  $\mu$  cr.; urediosporae ovate vel ellipsoideae, 21–23 (–26)  $\times$  (26–) 29–35 (–40)  $\mu$ ; membrana 1–1.5  $\mu$  cr., hyalina vel pallide flavida, moderate echinulata; poris germ. obscuris.

On *Vernonia amygdalina*, UGANDA: Rukungiri, Kigezi, Aug. 1937, *Hansford 2171* (TYPE).

This species is undoubtedly related to *Uredo vernonicola* Petch and *U. toroiana* Kern, both also on *Vernonia*, but differs because of larger urediospores.

**Uredo palpigera** Cummins, sp. nov. Urediis subepidermalibus, epiphyllis rarius hypophyllis, brunneis, in maculis brunneis sparsis vel laxe aggregatis, poro centrali apertis, rotundatis, 0.1–0.3 mm. diam.; paraphysibus plerumque periphericis, 1–2-septatis, plus minusve puccinioideis, cylindraceis vel clavatis, rectis vel incurvatis, deorsum conjunctis, hyalinis vel brunneis, 10–18  $\times$  45–115  $\mu$ ; membrana 1–2  $\mu$  cr. vel ad apicem usque 8  $\mu$  cr.; urediosporae late ellipsoideae vel ellipsoideae, 17–23  $\times$  25–29  $\mu$ ; membrana 1.5–2  $\mu$  cr., flavidula vel pallide flavo-brunnea, moderate tenuiter echinulata; poris germ. obscuris.

On *Inula acervata*, UGANDA: Kigezi, Aug. 1937, *Hansford 2150* (TYPE).

*Uredo brachylaenae* Doidge, which occurs on the genus *Brachylaena* of the tribe Inuleae, is probably similar but has smaller spores (15–17  $\times$  18–23.5  $\mu$ ). These two species are morphologically similar to *U. perscita*, *U. toroiana* and *U. vernonicola* and perhaps all will be found to belong in the genus *Phakopsora*. Hiratsuka (Bot. Mag. Tokyo **49**: 854. 1935) has recently transferred *Uredo elephantopodis*, a species with similar morphology, to *Phakopsora*.

**Aecidium entebbense** Cummins, sp. nov. Pycniis epiphyllis, aggregatis, brunneis, subcuticularibus, lenticularis 50–70  $\mu$  altis, 110–170  $\mu$  latis. Aecii hypophyllis, subepidermalibus, in maculis pallide brunneis usque ad 1.5 cm. dense aggregatis, cupulatis, 100–150  $\mu$  diam., margine albido, recurvato; cellulis peridii firme conjunctis, oblongis vel polyhedricis 13–19  $\times$  18–25  $\mu$ , pariete exteriori striato 3–3.5  $\mu$  cr., interiore verrucoso 2–3  $\mu$  cr.; aeciosporae globoideae, ellipsoideae vel oblongo-ellipsoideae, 13–18  $\times$  16–23  $\mu$ ; membrana 1  $\mu$  cr., ad apicem 3–8  $\mu$  cr., hyalina vel pallide flavida, verruculosa.

On *Phyllanthus discoideus*, UGANDA: Entebbe Road, June 1942, *Hansford 3016* (TYPE).

None of the species of *Aecidium* previously described on *Phyllanthus* has aeciospores with an apically thickened wall. One of these, *A. phyllanthi* P. Henn., occurs on *P. discoideus* in Africa. In addition to having aeciospores with uniform walls, it differs also in having hypophyllous pycnia. The pycnia in *A. entebbense* have a flat hymenium and are bordered by peridial tissue composed of long, narrow cells, as is frequently true of subcuticular pycnia.

**AECIDIUM EVANSII** P. Henn. On *Lippia* sp., UGANDA: Sabei, Elgon, December 1933, *Hansford 1678*.

Certain morphological features have not been sufficiently emphasized in published descriptions of this species. The walls of the aeciospores vary in thickness because of invaginations of the inner surface. These invaginations are numerous, frequently pronounced and occur both in the side and the apically thickened areas of the wall. This character is exhibited also by a specimen on *L. asperifolia* collected by Pole Evans in the Pretoria District of Transvaal (Mycol. Herb. Union Dept. Agr. no. 5186; identified by Miss

Doidge), in a specimen on *L. berlandieri* of uncertain origin (Mexico?), and can be considered characteristic of the species. In Hansford's specimen the aecia are cylindric, about 1 mm. in length, and tend to develop along the veins of the leaf.

*AECIDIUM VERNONIAE-PODOCOMAE* Doidge. On *Vernonia* sp., UGANDA: Kawanda, Kampala, June 1939, *Hansford 2475*.

This rust has not been recorded for Uganda. The specimen was received as ? *Aecidium vanderystianum* P. Henn. but has the thick-walled spores described by Doidge.

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## NEW COMBINATIONS IN CORNUS

H. W. RICKETT

The following nomenclatural changes in *Cornus* are proposed for the sake of consistency in a forthcoming treatment of the genus in North American Flora.

*CORNUS DRUMMONDI* f. **priceae** (Small) Rickett, comb. nov. *C. priceae* Small, *Torreyana* 1: 54. 1901. This form differs from typical *C. drummondii* (*C. asperifolia* of authors) only in the small size of the fruit. It has been reported only from the type locality.

*CORNUS FLORIDA* subsp. **urbiniiana** (Rose) Rickett, comb. nov. *C. urbiniana* Rose, Contr. U. S. Nat. Herb. 8: 53. 1903. *C. florida* var. *urbiniiana* Wangerin in Engler, Pflanzenreich IV. 229 (41): 87. 1910. The Mexican plants so designated differ from *C. florida* of the eastern United States in several minor characters: the narrow acute (not retuse) involueral bracts; fewer flowers in each inflorescence; usually only 1-3 fruits in a cluster. Such distinctions are scarcely of specific importance; were it not for the geographic disjunction, it would probably be impossible to segregate, on such bases, two independent populations. On the other hand, the two populations are at present perfectly distinct; and for this reason (as well as because of the rather anomalous status of the concept of *varietas*) it seems appropriate to consider them as subspecies.

*CORNUS DISCIFLORA* f. **floccosa** (Wangerin) Rickett, comb. nov. *C. floccosa* Wangerin, Repert. Sp. Nov. 6: 101. 1908. *C. disciflora* var. *floccosa* Standl. Field Mus. Publ. Bot. 8: 321. 1931. The leaves of typical *C. disciflora* are pubescent with very minute appressed forked trichomes. *C. disciflora* f. *floccosa* differs only in the short-tomentose, often ferruginous pubescence of the leaves. The two types of trichomes may be mixed in various proportions, so that leaves even on the same plant may differ in pubescence (thus recalling the distinction between *C. stolonifera* and its f. *baileyi*). The validity of the quantitative differences described by Wangerin in proposing his species must be tested by adequate study of the plants in the field.

*CORNUS STOLONIFERA* f. **flaviramea** (Späth) Rickett, comb. nov. *C. alba* var. *flaviramea* Späth ex Koehne, Mitt. Deuts. Dendr. Ges. 12: 39. 1903. *C. stolonifera* var. *flaviramea* Rehder in L. H. Bailey, Cycl. Am. Hort. 1: 377. 1900. Though the yellow-stemmed "red osier" dogwood is known only in cultivation, it may be sufficiently stable to need formal treatment. Obviously the distinction merits nothing more than the rank of *forma*.

THE NEW YORK BOTANICAL GARDEN  
NEW YORK

## INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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ESTIMATES OF THE MINIMUM NUMBERS OF GENES  
DIFFERENTIATING SEVERAL TAXONOMIC  
CATEGORIES IN THE GENUS  
SOLIDAGO\*

RICHARD H. GOODWIN

Intensive genetic investigations have shown that a very large number of distinct gene loci may be identified within a single species. In *Drosophila melanogaster*, for example, this figure undoubtedly exceeds 480 (Bridges & Brehme 1944); in maize, 300 (Emerson, Beadle & Fraser 1935). A large number of these genes, however, are recessives which appear only rarely in the wild. Cultivation and domestication drastically alter the forces normally operating upon a natural population, and special experimental methods have recently been employed (Dobzhansky & Epling 1944; Clausen, Keck & Hiesey 1940) to bring out latent genetic variability which normally would remain undetected. The total number of genes present within the nucleus and in operation during the development of any particular species has never been determined, and only very crude estimates have been hazarded at this figure.

Another type of estimate is of considerable interest, however. The vast array of organisms confronting the student of natural history has been studied and subdivided into a series of systematic categories—phylum, class, order, family, genus, species, subspecies, form, etc. The validity of the concept of descent with modification, resulting in natural relationships at various taxonomic levels, suggested by the above-mentioned terms, is universally accepted, although there is frequently a wide divergence of opinion with respect to the definition of these categories and their interpretation. The question which we wish to discuss here is the problem of estimating the number of gene loci involved in differentiating lines of descent at various taxonomic levels. At the present time the methods of getting at this problem are genetic and involve breeding experiments between related forms. Since intergeneric crosses are rare and usually sterile, estimates above the species level can only be made very exceptionally, and even at that level, can only be made in certain favorable cases. Estimates within a species can readily be obtained.

On the basis of genetic studies begun about ten years ago, minimal estimates have been made of the number of gene loci involved in differentiating a few lines of descent within the genus *Solidago*. Two of these lines are recognized as belonging to distinct species; two as distinct subspecies; and two as distinct strains of the same subspecies. The general procedure has been the

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collection of a few sample *Solidago* specimens from natural populations at widely separated geographic localities. These plants have been grown for a number of years in the greenhouse and also under field conditions in an experimental garden. During this period various character differences have been noted. Certain crosses have been made between these stock plants, and  $F_1$  and  $F_2$  hybrid populations have been raised and analysed.

Wright (in Castle 1921) has developed a method of estimating the number of gene substitutions which determine a difference in some measurable character between two isogenic strains, if numerous individuals of each strain and of their  $F_1$  and  $F_2$  have been measured with respect to that character. The method is indicated by the following formula, in which  $\bar{v}_p$  and  $\bar{v}_p$  represent the average measurements of the parental strains,  $\sigma_1$  and  $\sigma_2$  the standard deviations of the  $F_1$  and  $F_2$ , and  $n$  the number of gene differences:

$$n = \frac{(\bar{v}_p - \bar{v}_p)^2}{8(\sigma_2^2 - \sigma_1^2)}$$

This formula gives a minimal estimate and is based on the assumptions (1) that each strain is isogenic with respect to the character studied, (2) that the large-size genes are concentrated in one strain, the small-size genes in the other, (3) that the genes involved have equal or additive effects (at least upon proper choice of scale), without dominance or epistasis, and (4) that no two of the loci are in the same chromosome. If these assumptions do not match the actual conditions in the material to which the method is applied, the estimated number of gene differences will be smaller than the actual number. In any event a minimal estimate will be obtained.

In cases where more than one character is involved, some of the genes may have manifold effects. On the basis of assumptions 1, 3, and 4, mentioned above, the following formula for estimating the maximum number of genes influencing the phenotypic expression of any two characters has been derived (Charles and Goodwin 1943):

$$n_L (1 - 2c) + n_C = \frac{\Delta x \Delta y (r_2 R_x R_y - r_1)}{8(R_x^2 - 1)(R_y^2 - 1)}$$

where

$n_L$  = the number of character- $x$  loci each linked with a character- $y$  locus.

$c$  = the average crossover value between linked pairs of genes.

$n_C$  = the number of genes acting on both characters.

$\Delta x$  = the difference between parents in average value of character  $x$ , divided by the standard deviation of that character in  $F_1$ .

$\Delta y$  = the analogous quotient for character  $y$ .

$R_x$  = the standard deviation of character  $x$  in the  $F_2$ , divided by the standard deviation of character  $x$  in the  $F_1$ .

$R_y$  = the analogous character- $y$  quotient.

$r_1$  and  $r_2$  = the correlation coefficients between characters  $x$  and  $y$  in the  $F_1$  and  $F_2$  respectively.

The right-hand member of this formula may be computed for a given character pair, but there is no ready way to determine the proper values of the number of linked and the number of common genes. For purposes of making a *minimal* estimate of the total number of genes involved in a given cross, however, it is safe to take the value of the total common genes ( $n_c$ ) as equal to the nearest integer below the exact value for the combined expression  $n_L(1 - 2c) + n_c$ .

The biological material used in these studies belongs to two species complexes. The *Solidago rugosa* complex includes goldenrods of open woods and clearings, thickets, fencerows, and roadsides, and is widespread throughout eastern North America from Newfoundland to Texas. Fernald (1936) writes that "probably no aggregate-species of *Solidago* in America, unless it be the *canadensis* group, is more baffling in its variations than *S. rugosa* Mill." He then proceeds to delimit a series of races which he considers to be of subspecific rank. There is no question that much experimental work, patterned after the comprehensive studies of Clausen, Keck and Hiesey (1940), needs to be done to clarify the status and limits of this complex and its components, as will be exemplified by results to be discussed later in this paper. A single sample representing Fernald's *S. rugosa* var. *typica*<sup>1</sup> was collected in Belmont, Massachusetts, for experimental purposes.

*Solidago sempervirens*, as now interpreted by American authors, is a maritime species, growing in brackish marshes and along sandy or rocky shores all the way from Newfoundland to Mexico. It includes northern and southern races which are morphologically distinguishable, and which Linnaeus (1753), and others before him, regarded as being specifically distinct. Certain systematists (Small 1933; Friesner 1933; Buswell 1942) apparently regard the differences between these races as of no taxonomic significance. Fernald (1935), however, basing his decision upon field observations and herbarium studies, considers these forms to be pronounced "geographic varieties," of subspecific rank.<sup>1</sup> The range of the northern form, his var. *typica*, overlaps that of the southern var. *mexicana*, from Massachusetts to Virginia. In the region of overlap he states that the two subspecies appear to be ecologically separated, *typica* inhabiting the exposed, saline outer beaches, *mexicana* the sheltered, less saline estuaries and marshes. I have not made extensive field studies in this area myself, but consider that extensive collecting might prove very illuminating. Plants used in the present investigation were obtained from three stations along the coast. Var. *typica* was collected at Ipswich, Massachusetts; var. *mexicana*, from Ocean City, Maryland, and from Fort Myers, Florida.

Natural hybridization may occur between *S. rugosa* and *S. sempervirens*, where individuals of both species happen to grow in close proximity to one

<sup>1</sup> For a discussion of Fernald's use of the term variety, see R. T. Clausen (1941).

another. Favorable localities are rather infrequent and occur chiefly where ecological conditions have been upset by the hand of man (see Wiegand 1935). In one such locality which has been intensively studied (Goodwin 1937a, 1937c) extensive hybridization and backcrossing has resulted in an extremely polymorphic population.

Artificial crosses have been made between *S. sempervirens* and *S. rugosa*, and fertile  $F_1$  and  $F_2$  hybrids have been obtained (Goodwin 1937c). As might be expected, the number of chromosomes is the same in both species, and cytological studies reveal normal meiotic behavior in the  $F_1$  hybrids.

From a subsequent analysis of the parental and hybrid populations (Charles & Goodwin 1943) with respect to six differentiating leaf-characters, the numbers of genes determining each character difference, and maximal numbers of genes acting on both members of each character pair were estimated. It was concluded that a minimum of 21 genes might account for these character differences. Other morphological differences in the inflorescence and the vegetative axis were not analyzed. Some of them might be attributed to the manifold action of some of the 21 leaf-character genes; but it seems almost certain that the *actual* total number of gene substitutions involved in differentiating *S. sempervirens* from *S. rugosa* is considerably greater than this *minimal* estimate—possibly in the neighborhood of 40 genes.

From the foregoing discussion, it should be clear that *rugosa* and *sempervirens* are closely related members of a species complex in which species delimitation becomes a perplexing problem. Dobzhansky (1935) has defined a species as that stage of the evolutionary process "at which the once actually or potentially inter-breeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding." In an illuminating discussion of this definition in the concluding chapter of his book *Genetics and the Origin of Species* (1937), he makes the following statement which is applicable in the present case: "In some instances hybrids between species are observed mainly in localities modified by man's activity (Wiegand 1935). The physiological isolating mechanisms that have kept these species separate (presumably ecological isolation) prove inadequate when the conditions have changed due to the introduction of new factors. So long as a complete physiological isolation has not developed, the process of evolution is partly reversible: once discrete groups may become fused again into a single one." The foregoing genetic analysis has shown that the numerous morphological differences between *rugosa* and *sempervirens* are each controlled by a battery of genes. This indicates that speciation has reached a fairly advanced stage. To reduce *rugosa* and *sempervirens* to two very dissimilar ecotypes (Turesson 1922) of the same species would do violence to the species delimitations of these goldenrods as interpreted by every taxonomist who has worked with the genus to date.

TABLE 1. *Floret number and fruit length in S. sempervirens vars. typica and mexicana.*  
Means and standard deviations are given when available. Extremes are in parentheses.

Source of material	Number of ray florets	Number of disc florets	Total florets	Fruit length in mm.	Authority
<i>var. typica</i>					
Gray's Manual	(7-10) <sup>a</sup>	about 15 <sup>a</sup>			Friesner (1933)
Range					Fernald (1935)
Massachusetts	11.5 (7-15)	14.5 (11-20)	26 (20-33)	2.9 (2.2-3.5) <sup>a</sup>	Goodwin (1937c)
Massachusetts <sup>b</sup>	11.3 ± 2.6 (7-17)	15.0 ± 3.8 (9-25)	26.1 ± 5.6 (16-41)	2.92 ± 0.31 (2.3-3.7)	Goodwin & Cahill
<i>var. mexicana</i>					
Maryland <sup>b</sup>	8.3 ± 1.2 (7-10)	9.8 ± 1.7 (7-12)	18.1 ± 2.0 (14-21)	2.48 ± 0.50 (2.2-3.2)	Goodwin & Cahill
Florida	(8-11)	(8-15)			Buswell (1942)
Florida <sup>b</sup>	7.8 ± 1.4 (5-11)	8.2 ± 1.7 (6-11)	15.7 ± 1.4 (13-22)	2.26 ± 0.20 (1.7-2.7)	Goodwin & Cahill

<sup>a</sup> Figures intended to be representative of *var. typica*. Friesner's figures for the number of ray florets were probably taken from Gray's New Manual of Botany, 7th ed., 1908.

<sup>b</sup> Plants grown in the greenhouse at Rochester, New York.

TABLE 2. Total number of florets per head in two strains of *S. sempervirens* and their  $F_1$  and  $F_2$  progeny.  
Two heads were counted per plant and the values averaged.

Cross	12-13	14-15	16-17	18-19	20-21	22-23	24-25	26-27	28-29	30-31	32-33	34-35	36-37	38-39	40-41	No. of plants	Aver. No. of florets	$\sigma$
Mass.	1	3	5	2	2	3	2	5	1	0	2	1	1	1	1	19	26.1	$\pm 2.2$
Fla.	1	1	1	1	5	16	15	11	2	2	1					10	15.7	$\pm 0.9$
$F_1$	1	1	1	10	9	19	15	11	1	2	1			1		50	27.0	$\pm 2.4$
$F_2$																71	23.2	$\pm 3.7$

TABLE 3. Fruit length, exclusive of pappus, in mm. in two strains of *S. sempervirens* and their  $F_1$  and  $F_2$  progeny.  
Ten fruits were measured per plant and the values averaged.

Cross	2.05	2.15	2.25	2.35	2.45	2.55	2.65	2.75	2.85	2.95	3.05	3.15	3.25	3.35	3.45	No. of plants	Aver. age length	$\sigma$
Mass.		3	5			1	3	3	2	2	4	1	1	1	1	18	2.92	$\pm 0.25$
Fla.					2	1	1	6	8	8	6	2	1			10	2.26	$\pm 0.10$
$F_1$		1	6	1	6	6	15	7	7	4						39	2.84	$\pm 0.18$
$F_2$	1	6	1	6	6	6						2				61	2.60	$\pm 0.25$

Passing now to a consideration of the species *S. sempervirens* itself, crosses have been readily obtained between the northern subsp. *typica* from Massachusetts and samples of the southern subsp. *mexicana* from Maryland and Florida. These two groups appear to differ in a number of characters, some of which, such as growth-rate, length of stem and amount of anthocyanin in the leaves, are rather unfavorable for study. Two morphological characters in the inflorescence, however, the number of florets per head and the length of the mature fruit, lend themselves to analysis. The nature of the differences are indicated in table 1. It may be noted that the Maryland material of *mexicana* is somewhat less different from *typica* than the Florida material, suggesting some genic interchange in the zone of overlap between the two subspecies.

TABLE 4. Correlations between pairs of characters in  $F_1$  and  $F_2$  populations derived from crosses between Massachusetts and Florida strains of *S. sempervirens*, with an index which is equal to the number of genes acting on both characters plus a function of the number of linked gene pairs (one gene of each pair affecting one character, one the other).

Character pair	Correlation in		Common gene index
	$F_1$	$F_2$	
Number of florets; seed length	+ 0.056	+ 0.178	0.5
Number of florets; date of bud initiation	- 0.119	- 0.476	2.1
Number of florets; number of days from bud initiation to anthesis	+ 0.043	+ 0.008	0.0
Seed length; date of bud initiation	- 0.002	- 0.045	0.3
Seed length; number of days from bud initiation to anthesis	- 0.128	- 0.469	1.4

The results of crosses between Massachusetts (Mass.) and Florida (Fla.) strains are given in tables 2 and 3.<sup>2</sup> From these data it has been estimated that differences in total floret-number and in fruit-length are each controlled by at least two genes, the exact value for  $n$  being 1.7 in each case. Apparently there is a minimum of four differentiating genes, since the computed common gene index (see table 4) indicates that there are no genes in common between these morphological characters.

A special study has been made of the inheritance of flowering time in the *sempervirens* complex. In its natural habitat this species flowers progressively later as one passes from north to south along the Atlantic seaboard. When plants from different portions of the range are grown at the same latitude under similar conditions, these plants still flower at different times, those from the north blooming earlier than those from the south. This has been interpreted as evidence for the existence within the species of a cline

<sup>2</sup> The flowering behavior of these same populations has previously been studied (Goodwin 1944). The author is indebted to Miss Ruth Cahill for her assistance in collecting material and the data presented in these tables.

or graded series of strains genetically distinguished from one another by their physiological requirements for floral initiation (Goodwin 1941). As a matter of fact, it has been demonstrated that the controlling environmental factor in floral initiation in this species is the length of the photoperiod (Allard & Garner 1940; Goodwin 1944). In the north, the species is able to initiate floral primordia in a relatively long day and short night, whereas in the southerly portions of the range, shorter days and longer nights are required. However, the flowering-time problem is further complicated by variations in the rate at which the buds develop, once they have become initiated.

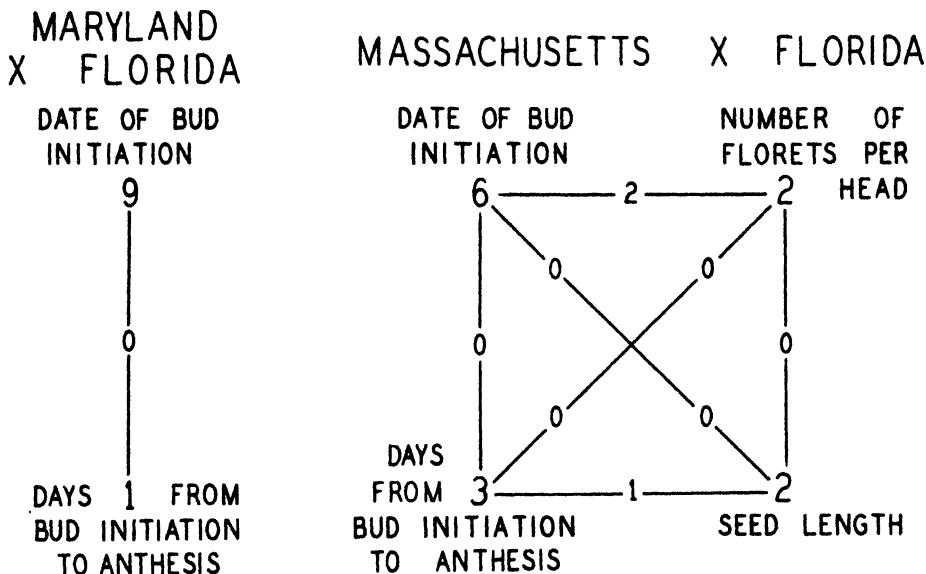


FIG. 1. Characters differentiating three strains of *S. sempervirens*, estimated minimal numbers of gene differences determining each character difference (larger digits), and maximal numbers of genes acting on both members of each character pair (digits on lines connecting the characters).

Crosses have been made between Massachusetts and Florida, and Maryland and Florida strains. From an analysis of the flowering behavior of the  $P_1$ ,  $F_1$ , and  $F_2$  generations derived from these crosses, estimates have been made of the numbers of genes differentiating these strains with respect to the date of floral initiation and the number of days elapsing between floral initiation and anthesis (Goodwin 1944). A minimum of nine or ten flowering-time genes appears to be involved. These estimates are presented in figure 1, together with those for the morphological characters in the Massachusetts  $\times$  Florida cross. The maximum numbers of genes which might be held in common between these morphological and physiological characters (data from table 4 and Goodwin 1944, table 5) are also shown.



Table 5 gives a summary of the minimum numbers of genes estimated to be differentiating the various strains which have thus far been studied. A distinction has been drawn between morphological characters, which have been useful to the systematist, and physiological characters, which have been of little practical value. It should be pointed out that no assessment of physiological genes has been made in the *rugosa*  $\times$  *sempervirens* cross. There are doubtless quite a number in operation (see Goodwin 1937b, 1937d).

The large number of morphological genes differentiating the two species is in marked contrast to the small number differentiating the two subspecies. These results are in agreement with those of other investigators such as Honing (1923) and Baur (1932) who have found that distinct species which are sufficiently closely related to yield fertile hybrids are differentiated by many genes. Fabergé (1943) in a recent analysis of the alpine poppies finds the genetic differences between specific categories to be multifactorial; the

TABLE 5. *Estimates of the minimum numbers of differentiating genes in Solidago crosses.*

Cross	Morpho- logical characters	Physio- logical characters	Total
<i>rugosa</i> var. <i>typica</i> $\times$ <i>sempervirens</i> var. <i>typica</i>	21	0	21
<i>sempervirens</i> var. <i>typica</i> (Mass.) $\times$ <i>sempervirens</i> var. <i>mexicana</i> (Fla.)	4	9	10
<i>sempervirens</i> var. <i>mexicana</i> (Md.) $\times$ <i>sempervirens</i> var. <i>mexicana</i> (Fla.)	0	10	10

subspecific categories, mostly or entirely monogenic. Between species he states "that there are many other genic differences giving rise to less clear-cut phenotypic characters, which have not been recorded"; but he also expresses the opinion that in this group the taxonomists have drawn their specific distinctions too fine.

Detailed comparative studies of strains within natural groups of organisms, such as those reported by Turesson (1930), Evans (1939), Clausen, Keck and Hiesey (1940), Dobzhansky and Epling (1944), Olmsted (1944) and Goodwin (1944), bring to light numerous physiological differences. These differences may be controlled by rather large numbers of genes, as indicated by the *Solidago* studies reported in this paper.

It seems unlikely that estimates of the total numbers of genes differentiating groups of organisms are going to be of much use to systematists in the immediate future. Key characters will undoubtedly continue to be selected chiefly on the basis of practical considerations, and morphological characters will continue to be favored over physiological, as taxonomic criteria. Furthermore, there are many other variables, such as differences in the quality and

magnitude of the phenotypic effects of genes, which may also decrease the taxonomic value of numerical estimates.

In spite of these facts, studies of the type reported here represent contributions toward our understanding of the genetic complexity responsible for specific and subspecific differentiation in groups of organisms. However little value they may have for the systematist, these studies should be of significance to the student interested in the mechanics of speciation.

#### SUMMARY

Interspecific and intraspecific crosses in *Solidago* have been made between various strains. From analyses of the  $F_1$  and  $F_2$  populations, estimates have been made of the minimal numbers of genes differentiating these strains.

Taxonomic distinctions in this genus have been based upon morphological criteria. The number of genes involved in the control of some of the morphological differences in an interspecific cross has been estimated to be at least 21; in an intraspecific cross, between strains which have been considered subspecifically distinct, at least four.

For practical reasons the systematist has taken little cognizance of physiological behavior in delimiting taxonomic categories. Yet in the two intraspecific crosses studied, at least nine or ten genes appear to be involved in differentiating the parental strains with respect to flowering time. In one case, the strains were morphologically dissimilar and subspecifically distinct; in the other case, morphological differences were inadequate to warrant a taxonomic separation.

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## THE VALIDITY OF THE ALGAL GENUS THAMNIASTRUM<sup>1</sup>

CLARENCE E. TAFT

The genus *Thamniastrum* described from Massachusetts by Reinsch (1888) has been accepted by many as a valid genus. The failure of its rediscovery has led others, Collins (1909), Printz (1927) and Smith (1933) to question its validity. Although the failure to rediscover an organism over a period of fifty years or more does not necessarily invalidate it, it does invite questions as to its legitimacy.

In this instance the writer believes that *Thamniastrum* is not a valid genus, and that Reinsch saw and figured the central, branching stalk system

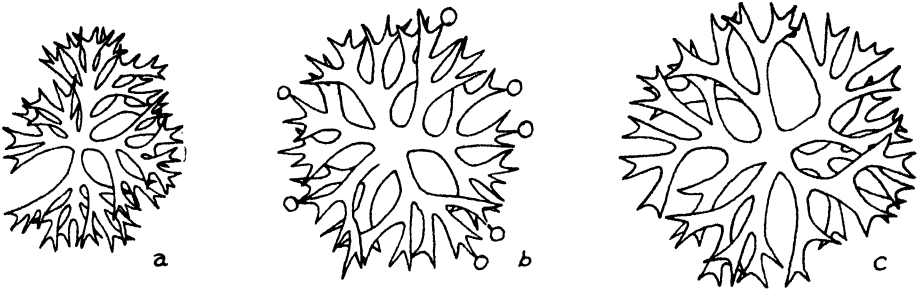


FIG. 1. a, The figure of *Thamniastrum* as published by Reinsch in 1888. b, The stalk system of *Gomphosphaeria lacustris* with a few cells attached. c, The stalk system of *Gomphosphaeria lacustris*.

of a colony of the blue green alga *Gomphosphaeria*. Material collected by the writer in Lake 16, Section 16 Presque Isle County, Michigan, during the summer of 1936, appears to support this contention. Collections from this lake contained numerous structures which were readily identified on the basis of shape as *Thamniastrum*. The color of the "cells" was a very pale green or blue green with transmitted yellow light. Although no cell contents could be recognized, camera lucida drawings were made and the identification assumed as no other alga had this peculiar organization. In the same collection, however, there were numerous colonies of *Gomphosphaeria lacustris*. An examination of these showed that in many instances the outer, more watery gelatinous envelope of the colony had disintegrated, allowing the cells to break away. This disintegration which was probably due to the exceptionally high temperature of the lake water had, in some instances continued until only a very few cells remained attached to the radiately branched, central

<sup>1</sup> Papers from the Department of Botany, The Ohio State University, No. 476.

mass, or stalk system. In every case, the central stalk system was identical in appearance with the previously identified *Thamniastrum*.

The similarities which exist between the figures of *Thamniastrum* and the stalk system of *Gomphosphaeria* are evident in the accompanying figures. Fig. 1a is that of *Thamniastrum* as published by Reinsch in 1888. Fig. 1b is the stalk system of *Gomphosphaeria* from which the outer, watery colonial envelope, as well as most of the cells, has disappeared. Fig. 1c is the central stalk system of *Gomphosphaeria* from which all cells and the outer envelope have disappeared.

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## THOMAS JEFFERSON

## HIS INTEREST IN PLANT LIFE AS REVEALED IN HIS WRITINGS—II\*

EDMUND H. FULLING

## BOTANY

Jefferson's relation to botany, distinguished as a pure science from the more utilitarian practices of agriculture and the more aesthetic art of gardening, was primarily that of patron and sponsor rather than that of devotee by either profession or avocation. He took occasions to express himself, however, as we shall note, with regard to certain biological principles, and in his famous *Notes on the state of Virginia* he left a compendium of scientific observations that might be the envy of any investigator. More important, however, were his sponsorship of a famous expedition and his advocacy of botanical and agricultural studies in university curricula. These aspects of his activities will now occupy our attention, and in conclusion we shall note the genus of plants named after him in recognition of his erudition in matters of natural history.

## TAXONOMY AND NOMENCLATURE

As we have already observed in considerable detail, Jefferson's interest in American agriculture was very much stimulated during his residence in France by the farming practices of the peasants there and in Italy; and a little later we shall give attention to his concern for exploration, also stimulated by a perspective gained abroad. It is not surprising, therefore, that on one occasion when writing from Paris to the President of Harvard, he should have exclaimed:

"What a field have we at our doors to signalize ourselves in! The Botany of America is far from being exhausted."<sup>1</sup>

He had in mind, of course, the natural flora of North America, the study of which had scarcely begun. Taxonomic concepts and nomenclature at that time were in a state of great change, and the influence of Linnaeus was just beginning to sift into the thoughts of American naturalists. Only 36 years had elapsed since the publication of Linnaeus' *Species Plantarum*, and comparisons were still being made by those who knew anything about the matter, not merely from a historical standpoint but respecting their debatable merits, between his artificial scheme of arrangement and other systems of classifica-

\* Part I of this series appeared in Bull. Torrey Club 71: 563-598.

<sup>1</sup> Letter to Dr. Willard, March 24, 1789 (13, VII, 325).

tion, especially the natural one of Jussieu. It is significant, therefore, that Jefferson was acquainted with the unsettled state of such abstract topics as were involved in this transition, and that he should have been called upon, several years after his retirement from the Presidency, for an opinion in the matter:

“The opinion which . . . you are pleased to ask of me, on the comparative merits of the different methods of classification adopted by different writers on Natural History, is one which I could not have given satisfactorily, even at the earlier period at which the subject was more familiar; still less, after a life of continued occupation in civil concerns has so much withdrawn me from studies of that kind . . . Nature has, in truth, produced units only through all her works. Classes, orders, genera, species, are not of her work. Her creation is of individuals . . . No two animals are exactly alike; no two plants, nor even two leaves or blades of grass . . . This infinitude of units or individuals being far beyond the capacity of our memory, we are obliged, in aid of that, to distribute them into masses, throwing into each of these all the individuals which have a certain degree of resemblance; to subdivide these again into smaller groups, according to certain points of dissimilitude observable in them, and so on until we have formed what we call a system of classes, orders, genera and species. In doing this, we fix arbitrarily on such characteristic resemblances and differences as seem to us most prominent and invariable in the several subjects, and most likely to take a strong hold in our memories. Thus Ray formed one classification on such lines of division as struck him most favorably; Klein adopted another; Brisson a third, and other naturalists other designations, till Linnaeus appeared. Fortunately for science, he conceived in the three kingdoms of nature, modes of classification which obtained the approbation of the learned of all nations. His system was accordingly adopted by all, and united all in a general language. It offered the three great desiderata: First, of aiding the memory to retain a knowledge of the productions of nature. Secondly, of rallying all to the same names for the same objects, so that they could communicate understandingly on them. And thirdly, of enabling them, when a subject was first presented, to trace it by its character up to the conventional name by which it was agreed to be called. This classification was indeed liable to the imperfection of bringing into the same group individuals which, though resembling in the characteristics adopted by the author for his classification, yet have strong marks of dissimilitude in other respects. But to this objection every mode of classification must be liable, because the plan of creation is inscrutable to our limited faculties. Nature has not arranged her productions on a single and direct line. They branch at every step, and in every direction, and he who attempts to reduce them into departments, is left to do it by the lines of his own fancy. The objection of bringing together what are disparata in nature, lies against the classification of Blumenbach and of Cuvier, as well as that of Linnaeus, and must forever lie against all. Perhaps not in equal degree; on this I do not pronounce. But neither is this so important a consideration as that of uniting all nations under one language in Natural History. This had been happily effected by Linnaeus, and can scarcely be hoped for a second time. Nothing indeed is so desperate as to make all mankind agree in giving up a language they possess, for one which they have to learn. The attempt leads di-

rectly to the confusion of the tongues of Babel. Disciples of Linnaeus, of Blumenbach, and of Cuvier, exclusively possessing their own nomenclatures, can no longer communicate intelligibly with one another. However much, therefore, we are indebted to both these naturalists, and to Cuvier especially, for the valuable additions they have made to the sciences of nature, I cannot say they have rendered her a service in this attempt to innovate in the settled nomenclature of her productions; on the contrary, I think it will be a check on the progress of science, greater or less, in proportion as their schemes shall more or less prevail. They would have rendered greater service by holding fast to the system on which we had once all agreed, and by inserting into that such new genera, orders, or even classes, as new discoveries shall call for. Their systems, too, and especially that of Blumenbach, are liable to the objection of giving too much into the province of anatomy. It may be said, indeed, that anatomy is a part of natural history. In the broad sense of the word, it certainly is. In that sense, however, it would comprehend all the natural sciences, every created thing being a subject of natural history in extenso. But in the subdivisions of general science, as has been observed in the particular one of natural history, it has been necessary to draw arbitrary lines, in order to accommodate our limited views. According to these, as soon as the structure of any natural production is destroyed by art, it ceases to be a subject of natural history, and enters into the domain ascribed to chemistry, to pharmacy, to anatomy, etc. Linnaeus' method was liable to this objection so far as it required the aid of anatomical dissection . . . It would certainly be better to adopt as much as possible such exterior and visible characters as every traveller is competent to observe, to ascertain and to relate. But with this objection, lying but in a small degree, Linnaeus' method was received, understood, and conventionally settled among the learned, and was even getting into common use. To disturb it then was unfortunate. The new system attempted in botany, by Jussieu, in mineralogy by Haüy, are subjects of the same regret, and so also the no-system of Buffon, the great advocate of individualism in opposition to classification. He would carry us back to the days and to the confusion of Aristotle and Pliny, give up the improvements of twenty centuries, and co-operate with the neologists in rendering the science of one generation useless to the next by perpetual changes of its language. In botany, Willdenow and Persoon have incorporated into Linnaeus the new discovered plants."<sup>2</sup>

In the foregoing opinion and in his preferring to retain the unnatural system of Linnaeus despite its recognised shortcomings, we find not only an indication of Jefferson's antipathy to changes in existing methods of scientific nomenclature and terminology but also that unusual interest which he so constantly exhibited in matters wholly foreign to the man not primarily concerned in their pursuit. More remarkable, however, as revealed in that opinion, was Jefferson's grasp of certain abstruse principles underlying classification, of the concept that Nature makes only individuals and that man, merely for his own convenience, attempts to recognize finite groups among them. And who but Jefferson, except it be his contemporary Benja-

<sup>2</sup> Letter to Dr. John Manners, February 22, 1814 (13, XIV, 97).



min Franklin, would appreciate at that time the role of Linnaeus, or even know that he existed, and much less, know that there were such other scholars as Jussieu, Willdenow, Buffon, Persoon, Ray, Klein, Brisson, Blumenbach, Cuvier, and Haüy. If one must find some ground in that letter for criticism it would probably be that Jefferson apparently was unacquainted or at least not concerned with the question of "natural" vs. "artificial" classification, and did not foresee that phylogeny would eventually provide the universally accepted basis.

#### PLANT PHYSIOLOGY

In the realm of plant physiology, too, Jefferson was reluctant to accept new ideas as soon as they were proposed, and in this respect he failed to reveal that foresighted recognition of advancement and truth which characterized so much of his other thought. In 1772 Priestley had been the first to note that green plants produce oxygen, and two years later Ingen-Housz, in forsaking certain previous ideas, claimed that sunlight had much to do with this process. Jefferson, however, though he is to be admired merely for knowing that the assimilatory and respiratory functions of green plants were being investigated, wanted further proof of this function before relinquishing earlier notions, and in writing from Paris to the President of William and Mary College, at Williamsburg, he commented:

"You know also that Dr. Ingenhousz had discovered, as he supposed, that vegetation might be promoted by occasioning streams of the electrical fluid to pass through a plant, and that other physicians had received and confirmed this theory. He now, however, retracts it, and finds by more decisive experiments, that the electrical fluid can neither retard nor forward vegetation. Uncorrected still of the rage of drawing general conclusions from partial and equivocal observations, he hazards the opinion that *light* promotes vegetation. I have heretofore supposed from observation, that light affects the color of living bodies, whether vegetable or animal; but that either the one or the other receives nutriment from that fluid must be permitted to be doubted of, till better confirmed by observation."<sup>3</sup>

Jefferson believed that "it is by the assistance of heat and moisture, that vegetables are elaborated from the elements of earth, air, water, and fire,"<sup>4</sup> a thought which, as Dr. Brown has observed, might have been taken from Aristotle or Pliny. And the role of legumes in restoring fertility to his depleted soil at Monticello was no better understood; Jefferson thought they served primarily in preserving a suitable physical condition in the soil.

Jefferson's false notions in these three and any other aspects of plant physiology which he may have held were, for the most part, reflections of what was known at the time concerning the functions of plants. Had photo-

<sup>3</sup> Letter to Bishop James Madison, July 19, 1788 (13, VII, 73).

<sup>4</sup> (13, II, 62).

synthesis, nitrification, and the role of chemical elements in the life of plants been better understood, it is safe to assume that Jefferson would have been familiar with at least the fundamentals of these processes as we now understand them.

“NOTES ON THE STATE OF VIRGINIA”

Jefferson's principal literary work, apart from his political writings, was his *Notes on the state of Virginia*. This contribution, covering 261 pages of his “Writings” (13), was an account of many topics written in response to requests from the Marquis de Barbe-Marbois, Secretary of the French Legation in Philadelphia, for information of many kinds desired by the latter's government. It was begun in 1781 and privately printed in Paris in 1784–1785 during Jefferson's residence there, but dated 1782. That original edition of 200 copies was followed at various times by French, English, German and numerous American editions. Virginia at that time, it must be remembered, was larger than at present, including what today are the States of Virginia, West Virginia, and Kentucky. Jefferson divided his notes into queries, and under Query VI, entitled “A Notice of the Mines and other Subterranean riches; its trees, plants, fruits, etc.,” he began his botanical discussion by commenting that:

“A complete catalogue of the trees, plants, fruits, &, is probably not desired. I will sketch out those which would principally attract notice, as being first, Medicinal; second, Esculent; third, ornamental; or four, useful for fabrication; adding the Linnaean system to the popular names, as the latter might not convey precise information to a foreigner. I shall confine myself, too, to native plants.”<sup>5</sup>

Jefferson then listed 129 plants in the four categories, with popular names and Linnaean equivalents for nearly every one. In connection with one of the half-dozen or so for which he did not give Latin names he added the following explanation and thereby not only again revealed his appreciation of nomenclature and his acquaintance with recognized authorities of his day, but, in the opinion of the late Professor True (27), actually started the nomenclatural history of the tree concerned:

“Paccan, or Illinois nut. Not described by Linnaeus, Millar, or Clayton. Were I to venture to describe this, speaking of the fruit from memory, and of the leaf from plants of two years' growth, I should specify it as *Juglans alba, foliolis lanceolatis, acuminatis, serratis, tomentosis, fructu minore, ovato, compresso, vir insculpto, dulci, putamine tenerrimo*. It grows on the Illinois, Wabash, Ohio and Mississippi. It is spoken of by Don Ulloa under the name of Pacanos, in his *Noticias Americanas*.”<sup>6</sup>

A year after the appearance of this account in 1784, Humphrey Marshall published a description of the same tree in his *Arbustrum Americanum*, and

<sup>5</sup> (13, II, 49).

<sup>6</sup> (13, II, 51).

there bestowed upon it the name *Juglans pecan*. Marshall's description, however, in Professor True's judgment, failed to distinguish the pecan from the pig-nut hickory, and "the name proposed by him is left so nearly nude that its title to priority is doubtful. The earlier, clean-cut, adequate diagnosis by Jefferson, can only on bibliographic technicality fail to secure for him the credit of being the first scientific sponsor for the pecan" (27). However valid or otherwise the claims for Jeffersonian priority in this matter may be in the minds of nomenclaturists and taxonomists today, the interesting fact remains that Jefferson was sufficiently interested in the tree and versed in a botanical approach to it that he recognized it as unnamed by the authorities of the time—Linnaeus, Miller, Clayton—and therefore endeavored to bring it within the fold of scientific recognition. For 25 years the tree had been known to other American naturalists, including John Bartram, but none had ventured to name it. As we have already noted, Jefferson attempted to introduce its cultivation into France, and in his correspondence concerning the tree, he recognized Marshall's name as official but spelled it *Juglans Paccan*.<sup>7</sup>

Jefferson realized that the list of plants in his *Notes* did not by any means include all the plants of Virginia, and he therefore referred his readers for further information to "Dr. Clayton's" *Flora Virginiana*, published by Gronovius at Leyden in 1762. Later, in an appendix to his *Notes*, he was induced to add to that list what we today know as Jimson weed by way of corruption of its original name of Jamestown weed:

"There is a plant, or a weed, called the Jamestown weed, of a very singular quality. The late Dr. Bond informed me, that he had under his care a patient, a young girl, who had put the seeds of this plant into her eye, which dilated the pupil to such a degree, that she could see in the dark, but in the light was almost blind. The effect that the leaves had when eaten by a ship's crew that arrived at Jamestown, are well known."<sup>8</sup>

In a footnote, Jefferson then referred to a mention which he found of an instance of temporary imbecility caused by these seeds. More interesting, however, in connection with this plant, is Jefferson's reference to it in one of his letters. His correspondent had sent him a supply of capsicum which he hoped to find hardy enough for growth in the climate of his neighborhood, species previously tried having been too tender. His correspondent had sent him also some "galvance"<sup>9</sup> which appeared to be different from what was generally cultivated under that name. In view of his having so many grandchildren and others about him, however, who might have been endangered by the poisonous plant, Jefferson regarded the risk as overbalancing his curiosity to experiment with it, and he impliedly made no attempt to grow it.

<sup>7</sup> Letter to Francis Hopkinson, December 23, 1786 (13, VI, 20).

<sup>8</sup> (13, II, 267).

<sup>9</sup> A variety of edible pea.

But he seems to have recognised virtues in its lethal nature, and to have advocated euthanasia, for he wrote elsewhere, in referring to deadly drugs:

"The most elegant thing of that kind known is a preparation of the Jamestown weed, *Datura-Stramonium*, invented by the French in the time of Robespierre. Every man of firmness carried it constantly in his pocket to anticipate the guillotine. It brings on the sleep of death as quietly as fatigue does the ordinary sleep, without the least struggle or motion. Condorcet, who had recourse to it, was found lifeless on his bed a few minutes after his landlady had left him there, and even the slipper which she had observed half suspended on his foot, was not shaken off. It seems far preferable to the Venesection of the Romans, the Hemlock of the Greeks, and the Opium of the Turks. I have never been able to learn what the preparation is, other than a strong concentration of its lethiferous principle. Could such a medicament be restrained to self-administration, it ought not to be kept secret. There are ills in life as desperate as intolerable, to which it would be a rational relief, e.g., the inveterate cancer. As a relief from tyranny indeed, for which the Romans resorted to it in the times of the emperors, it has been a wonder to me that they did not consider a poignard in the breast of the tyrant as a better remedy."<sup>10</sup>

Our interest in Jefferson's *Notes* lies not only in his enumeration of species and in his original observations on the pecan, but also in his appreciation of the value of scientific names. Undoubtedly, to the average man of his time, as to the layman of today, unconcerned with universality of knowledge, technical names constituted a superfluity. Jefferson, however, internationally minded as he was in scientific matters, wanted the "foreigner," as he expressed it, to know which plants he was writing about. He undoubtedly always had in mind the French savants, for, as we have already indicated, it was especially for them that his *Notes* were assembled. Similar understanding on his part is revealed when he says, in referring to tobacco, maize, round potatoes, pumpkins, cymplings, and squashes found by the English settlers in Virginia:

"it is not said whether of spontaneous growth, or by cultivation only. Most probably they were natives of more southern climates, and handed along the continent from one nation to another of the savages."<sup>11</sup>

His recognition of introduced plants is then expanded in a manner which throws much light on the kinds of crops being raised in Virginia:

"Besides these plants, which are native, our Farms produce wheat, rye, barley, oats, buck-wheat, broom corn, and Indian corn. The climate suits rice well enough, wherever the lands do. Tobacco, hemp, flax, and cotton, are staple commodities. The silk-worm is a native, and the mulberry, proper for its food, grows kindly. Indigo yields two cuttings.

"We cultivate, also, potatoes, both the long and the round, turnips, carrots, parsnips, pumpkins, and ground nuts (*Arachis*). Our grasses are lucerne,

<sup>10</sup> Letters to Dr. Samuel Brown, July 14, 1813 (13, XIII, 310).

<sup>11</sup> (13, II, 53).

St. Foin, burnet, ray(?), and orchard grass; red, white, and yellow clover; greensward, blue grass, and crab grass.

"The gardens yield musk-melons, water-melons, tomatoes, okra, pomegranates, figs, and the esculent plants of Europe.

"The orchards produce apples, pears, cherries, quinces, peaches, nectarines, apricots, almonds, and plums."<sup>12</sup>

It is from a letter written many years later, however, that we learn how well informed Jefferson was on purely academic aspects of introduced plants. At that time he had occasion to acknowledge receipt of a copy of a "General Geography" from the author of the volume, and after expressing thanks for the tome, he indulged in a little book-reviewing:

"In passing my eye rapidly over parts of the book, I was struck with two passages, on which I will make observations, not doubting your wish, in any future edition, to render the work as accurate as you can. In page 186 you say the potato is a native of the United States. I presume you speak of the Irish potato. I have inquired much into the question, and think I can assure you that plant is not a native of North America. Zimmerman, in his "Geographical Zoology," says it is a native of Guiana; and Clavigero, that the Mexicans got it from South America, its native country. The most probable account I have been able to collect is, that a vessel of Sir Walter Raleigh's, returning from Guiana, put into the west of Ireland in distress, having on board some potatoes which they called earth-apples. That the season of the year, and circumstance of their being already sprouted, induced them to give them all out there, and they were no more heard or thought of, till they had been spread considerably into that island, whence they were carried over into England, and therefore called the Irish potato. From England they came to the United States, bringing their name with them."<sup>13</sup>

Jefferson gave considerable thought to climatological conditions in his *Notes* and was much concerned with their bearing upon plant life. At one point, for instance, he referred to the reports of travelers that the climate west of the Alleghany Mountains was warmer than east of them along the same latitude, and observed that:

"Their testimony is strengthened by the vegetables and animals which subsist and multiply there naturally, and do not on the sea-coast. Thus Catalpas grow spontaneously on the Mississippi, as far as the latitude 37°, and reeds as far as 38°."<sup>14</sup>

Continuing his climatological observations, he then informed his French readers that:

"White frosts are frequent when the thermometer is at 47°, have killed young plants of Indian corn at 48° . . . I have known frosts so severe as to kill the hickory trees round about Monticello, and yet not injure the tender fruit blossoms then in bloom on the top and higher parts of the mountain;

<sup>12</sup> (13, II, 54).

<sup>13</sup> Letter to Horatio G. Spafford, May 14, 1809 (13, XII, 278).

<sup>14</sup> (13, II, 106).

and in the course of forty years, during which it had been settled, there have been but two instances of a general loss of fruit on it; while in the circumjacent country, the fruit has escaped but twice in the last seven years. The plants of tobacco, which grow from the roots of those which have been cut off in the summer, are frequently green here at Christmas."<sup>15</sup>

"A more satisfactory estimate of our climate to some, may perhaps be formed, by noting the plants which grow here, subject, however, to be killed by our severest colds. These are the fig, pomegranate, artichoke, and European walnut. In mild winters, lettuce and endive require no shelter; but, generally, they need a slight covering. I do not know that the want of long moss, reed, myrtle, swamp laurel, holly, and cypress, in the upper country proceeds from a greater degree of cold, nor that they were ever killed with any degree of cold in the lower country. The aloe lived in Williamsburg, in the open air, through the severe winter of 1779, 1780."<sup>16</sup>

Elsewhere in his *Notes*, where they are concerned with the honey bee, Jefferson concluded that the Laplanders did not have honey, for it was reported that they ate pine bark, prepared in a certain way, instead of articles sweetened with sugar.<sup>17</sup>

Lastly, in considering the plant-life aspects of his *Notes*, we can not afford to overlook the statistics which Jefferson provided on the annual export of plant products from Virginia before the war between England and France:<sup>18</sup>

Tobacco .....	55,000 hhds. of 1,000 lbs. each	\$1,650,000	30d per hhd.
Wheat .....	800,000 bu.	666,666	5-6d per bu.
Maize .....	600,000 bu.	200,000	1/3d per bu.
Tar, pitch, turpentine .....	30,000 bbl.	40,000	1½d per bbl.
Flax seed, hemp, cotton .....	4,000 bbl.	8,000	
Peas .....	5,000 bu.	3,333	2/3d per bu.

And if we turn to Jefferson for comparable figures concerning all the States, he accommodates us in one of his letters to La Fayette with estimates of such exports and their values in Louis:<sup>19</sup>

	To Europe	To West Indies
	Louis	Louis
Wheat, 2,210,000 bu. ....	331,000	
Maize .....	30,000	61,000
Rice, 130,000 bbl. ....	189,350	70,650
Indigo .....	51,700	
Tobacco, 87,000 hhds. ....	1,306,000	
Flax seed .....	79,500	
Hemp .....	21,000	
Hops .....	216,500	

<sup>15</sup> (13, II, 113).

<sup>16</sup> (13, II, 114).

<sup>17</sup> (13, II, 104).

<sup>18</sup> (13, II, 231).

<sup>19</sup> Letter to La Fayette, July 17, 1786 (19, 37).

In connection with the foregoing observations in his *Notes* it is fitting to observe what Jefferson penned in his account of a visit to Saratoga, Stillwater, Bennington, and Forts William, Henry, George, Ticonderoga, and Crown Point, all famous in the revolutionary misfortunes of General Burgoyne:

“We were more pleased, however, with the botanical objects which continually presented themselves. Those either unknown or rare in Virginia, were the sugar maple in vast abundance. The silver fir, white pine, pitch pine, spruce pine, a shrub with decumbent stems, which they call juniper, an azalea, very different from the nudiflora, with very large clusters of flowers, more thickly set on the branches, of a deeper red, and high pink-fragrance. It is the richest shrub I have seen. The honey-suckle of the gardens growing wild on the banks of Lake George, the paper-birch, an aspen with a velvet leaf, a shrub-willow with downy catkins, a wild gooseberry, the wild cherry with single fruit, (not the bunch cherry) strawberries in abundance.”<sup>20</sup>

Professor True has pointed out, on the authority of someone else, that the azalea so enthusiastically referred to in this letter probably was *A. canadensis*, first formally described twelve years later in 1803 by Richard in Michaux’ “*Flora*,” and that “had Jefferson taken the trouble to give his observations the form of conventional descriptions, it is quite likely that his discoveries would have added several plants then new to science” (27).

#### LEWIS AND CLARK EXPEDITION

The culmination of Jefferson’s interest in scientific pursuits and the master stroke in his patronage of such enterprises, was his conception and successful sponsorship of the justly famous Lewis and Clark Expedition. History generally accords the honors of exploration—and rightly so—to those who endure the privations and hardships of traversing previously unexplored lands, to those who risk their lives, leave the comforts of home and display the genius for organization, supervision and initiative so necessary in such undertakings. The sponsoring scientific societies or patronizing millionaires are generally known only to a few and very often do not merit greater recognition. For the Lewis and Clark Expedition, however, history makes an exception, and in even the most elementary treatise on early American affairs one finds this expedition closely associated not only with the administration of Thomas Jefferson as President of the United States but also with the man himself. Other phases of his scientific interests discussed in this paper are not matters of common historical knowledge; the Lewis and Clark Expedition, however, is at least related to every school-boy in America; it is fitting, therefore, that we include in this chapter of Jefferson’s relation to pure botany an account of this project which was his greatest contribution to science.

<sup>20</sup> Letter to Thomas Mann Randolph, June 5, 1791 (13, VIII, 204).

As is true of most other elaborate and productive enterprises, this one, too, was not conceived and executed all at once. Jefferson had long been interested in the vast unexplored territory which lay west of the Mississippi, and this concern was nurtured during his residence in France, where, we are told, he purchased every available book relating to the exploration, geography, and history of North America. While there, serving as American representative after Franklin, he became acquainted with one John Ledyard, a Connecticut explorer who had been a companion of Captain Cook through Behring Straits and on his last fateful visit to the Sandwich Islands. Ledyard's adventurous nature was seeking new worlds to conquer, and Jefferson prevailed upon him to return home via Siberia, Alaska, and the west coast of America, and to explore the great unknown country of the American Northwest on his way eastward. Ledyard undertook this hazardous route and proceeded nearly to Kamchatka, where further progress was forbidden by the Empress of Russia. Thus, as Jefferson wrote, "failed the first attempt to explore the western part of our northern continent."<sup>21</sup>

In 1789 Jefferson returned to America, and in Washington's cabinet he became the first American Secretary of State. While serving in that capacity he proposed that an exploring party be sent into the Northwest. Nothing, apparently, resulted from the suggestion, for in 1792 we find him again reviving the project, this time before the American Philosophical Society. He wanted the Society to raise funds for engaging a competent scientist to explore the northwestern territory by ascending the Missouri River, crossing the mountains and descending to the Pacific. The Society, apparently, was favorably impressed by his appeal and decided to sponsor the project. In seeking for someone to conduct such an expedition, it accepted the proffered services of André Michaux, the skilled botanist and experienced explorer who at the time was in America in the services of the French government. The expedition was financed by subscriptions and Jefferson apparently contributed £50, for in his Account Book, under date of April 28, 1793, we find the note "pd.  $\frac{1}{4}$  of my subscription for Michaud's [sic] journey to Pacific sea 12.5." In Jefferson's instructions to Michaux regarding the latter's notes to be made, we find the following very interesting detail:

"The method of preserving your observations is left to yourself, according to the means which shall be in your power. It is only suggested that the noting them on the skin might be best for such as may be the most important, and that further details may be committed to the bark of the paper-birch, a substance which may not excite suspicions among the Indians, and little liable to injury from wet or other common accidents. By the means of the same substance you may perhaps find opportunities, from time to

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<sup>21</sup> Letter to Paul Allen, April 13, 1813 (13, XVIII, 140).



time, of communicating to the society information of your progress, and of the particulars you shall have noted."<sup>22</sup>

Michaux arranged his party and set out, but had proceeded only as far as Kentucky when he was overtaken by an order from the French Minister in Philadelphia to pursue his botanical explorations elsewhere and to abandon his proposed journey into the Northwest. "Thus," wrote Jefferson, "failed the second attempt for exploring that region"<sup>21</sup> and the American Philosophical Society was deprived of sponsoring what might have become one of the greatest botanical explorations in North America. This frustration did not, however, diminish Jefferson's interest in botanical exploration or in the particular accomplishments of Michaux & Son. Twenty-three years later, in the concluding sentence of a letter otherwise devoted to his retirement from the Presidency of the Philosophical Society, he suddenly takes pride in his acquisition of Michaux's writings, by stating:

"Of Michaux's work, I possess three volumes, or rather cahiers, one on Oaks, another on Beeches and Birches, and a third on Pines."<sup>23</sup>

A few years earlier he had written to Michaux himself:

"I have duly received your favor of Aug. 10 and, with it, your beautiful account of the pines & firs of our country, for which be pleased to accept my thanks. I sincerely wish the work may be prosecuted, & that the citizens of the U. S. may not be wanting in due encouragement to it. nothing should be spared which I could do to befriend it. accept my best wishes that you may enjoy health to continue your useful labors."<sup>24</sup>

Jefferson's next opportunity to promote his project did not come until his third year as President of the United States. It was in his confidential message to Congress on January 18, 1803, in connection with the renewal of the act establishing trading houses with the Indians. He wanted the provisions of that act extended to the tribes on the Missouri, and along with his appeal he resurrected his favorite scheme by recommending that an exploring party be sent to trace the Missouri River to its source, then to cross the divide and to proceed by the best water route to the Pacific. Congress approved the proposition and appropriated \$5,000 for its execution. Meriwether Lewis, who had unsuccessfully applied in 1792 for leadership of the ill-fated American Philosophical Society expedition and had since then become a Captain in the Army and Secretary to Jefferson, was appointed by the latter to lead the expedition, with Lieutenant William Clark as second in command. Lewis had renewed his request to lead the party, and having won Jefferson's confidence he obtained the appointment. The success of the

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<sup>22</sup> Instructions to Andrew Michaud for exploring the western boundary (13, XVII, 335).

<sup>23</sup> Letter to John Vaughan, February 5, 1815 (13, XIV, 239).

<sup>24</sup> Letter to M. Michaux, April 15, 1811 (17, 115).

project is a tribute not only to Lewis' able leadership but as well to Jefferson's judgment in selecting him.

The preliminary details, general instructions and many other phases of the trip are beyond our interest in this account, but the concern which Jefferson displayed in those preliminaries and instructions with respect to plant life are, of course, pertinent to this study.

We find, for instance, that Jefferson sent Lewis to Dr. B. S. Barton of the Philosophical Society in Philadelphia in order that Lewis might become better acquainted with the botanical aspects of his contemplated journey. Had Michaux been able to continue as the original leader, Jefferson would not have had any occasion to be disturbed concerning botanical and allied matters. Under the circumstances, however, he was forced to admit to Dr. Barton, in emphasizing the qualifications of Lewis, that:

"It was impossible to find a character who, to a complete science in Botany, Natural History, Mineralogy and Astronomy, joined the firmness of constitution and character, prudence, habits adapted to the woods, and familiarity with the Indian manners and character, requisite for this undertaking. All the latter qualifications Captain Lewis has. Although no regular botanist, etc., he possesses a remarkable store of accurate observation on all the subjects of the three kingdoms, and will, therefore, readily single out whatever presents itself new to him in either . . . In order to draw his attention at once to the objects most desirable, I must ask the favor of you to prepare for him a note of those in the lines of botany, zoology, or of Indian history, which you think most worthy of enquiry and observation."

This concern on the part of Jefferson for Lewis' being able to make proper observations and records was not just an incidental matter, for he concluded his letter to Barton by saying:

"I make no apology for this trouble, because I know that the same wish to promote science which has induced me to bring forward this proposition, will induce you to aid in promoting it."<sup>25</sup>

In his instructions to Lewis for conducting the expedition, the latter was admonished to note the agricultural practices of the Indians and the plants they used as food. The observation was also made that:

"Other objects worthy of notice will be, the soil and face of the country, its growth and vegetable productions, especially those not of the United States, . . . the dates at which particular plants put forth or lose their flower or leaf. . . ."<sup>26</sup>

On August 31, 1803, the expedition set out from Pittsburgh. After spending three winters en route, one of them on the Pacific Coast, it returned to St. Louis on September 23, 1806, where the party disbanded. Between those dates, the 30 or so persons who constituted this intrepid band of explorers

<sup>25</sup> Letter to Dr. B. S. Barton, February 27, 1803 (13, X, 366).

<sup>26</sup> Letter to Paul Allen, April 13, 1813 (13, XVIII, 140).

contributed to American history what will always remain one of the greatest if not the greatest feat of exploration in North America. Its most important result was wholly political in substantiating the new nation's claim to the Pacific Northwest. Its scientific results, too, were important, though, as a rule, they have been less emphasized, since most general historical accounts are political, rather than economic, social, or scientific.

On the way to the coast a collection of plants was made and then lost when it was deposited among other things somewhere at the foot of the Rocky Mountains. On the return trip another but less extensive collection was assembled, the subsequent history of which, until it was deposited in the Philadelphia Academy of Natural Sciences, involved many hardships. The task of describing the plants collected was given by Lewis through his friend Bernard McMahon to the English botanist Frederick Pursh who published an account of them in his *Flora Americae Septentrionalis* of 1814. Three subsequent commentaries on the collection and on Pursh's work in connection with it have appeared (22, 25, 26). To delve into the details of those three papers would be to go unjustifiably beyond the intended scope of the present writing into details which belong rather to the contributions of Lewis and certain botanists than to those of Jefferson. It suffices to note here that in his treatment of the 150 specimens submitted to him, Pursh referred to 119 different plants, many of which he described as wholly new. Through later work of other botanists, 183 distinct forms have been recognized (25).

Jefferson was more concerned with disposal of the seeds gathered by Lewis and with publication of the latter's journals. From several of his letters, including one to M. de la Cépède<sup>27</sup> of the National Institute of Paris, we learn that Jefferson entrusted the seeds collected by Lewis to a Mr. Hamilton, wealthy owner of the famous Philadelphia gardens known as "The Woodlands," and to Mr. Bernard McMahon, a botanist and nurseryman of the same city. He appears to have approached the latter as follows:

"Captain Lewis has brought a considerable number of seeds of plants peculiar to the countries he has visited. I have recommended him to confide principal shares of them to Mr. Hamilton of the Woodlands and yourself as persons most likely to take care of them, which he will accordingly do. He will carry them on to Philadelphia himself."<sup>28</sup>

Two months later Jefferson expressed further concern about the seeds:

"I am in hopes I am more fortunate in the seeds I now send you than (in) the effete roots before sent. The enclosed seeds are given me by Captain Lewis for my own garden, but as I am not in a situation to do them justice and am more anxious they should be saved in any way than merely to see them in my own possession, I forward them to you who can give them their best chance. It will give you too an opportunity of committing them earlier

<sup>27</sup> Letter to M. de la Cépède, July 14, 1809 (13, XII, 83).

<sup>28</sup> Letter to Bernard McMahon, January 6, 1807 (14, LIX, No. 67).

to the ground than those you will receive from Captain Lewis for yourself as it may yet be sometime before he is with you. perhaps you may as well say nothing of your receiving this list it might lessen the portion he will be disposed to give you; and believing myself they will be best in your hands, I wish to increase the portion deposited with you."<sup>29</sup>

Two days later Jefferson was induced by a change in Lewis' plans to write as follows, first to McMahon, than to Hamilton:

"Governor Lewis's journey to Philadelphia being delayed longer than was expected, and the season advancing, we have thought it best to forward to you by post the packet of seeds destined for you. they are the fruits of his journey across the continent and will I trust add some useful or agreeable varieties to what we now possess. I send a similar packet to Mr. Hamilton of the Woodlands. in making him and yourself the depositories of these public treasures, I am sure we take the best measures possible to insure them from being lost. I sent you a small packet a few days ago which he had destined for myself, but I am in too indifferent a situation to take the care of them which they merit."<sup>30</sup>

"it is with great pleasure that, at the request of Governor Lewis, I send you the seeds now enclosed, being a part of the Botanical fruits of his journey across the continent. I cannot but hope that some of them will be found to add useful or agreeable varieties to what we now possess. these with the descriptions of plants, which, not being in seed at the time, he could not bring, will add considerably to our Botanical possessions. he will equally add to the Natural history of our country. on the whole, the result confirms me in my first opinion that he was the fittest person in the world for such an expedition. he will be with you shortly at Philadelphia, where I have no doubt you will be so kind as to shew him those civilities which you so readily bestowed on worth. I send a similar packet to Mr. McMahon to take the chance of a double treatment in confiding these public deposits to your and his hands, I am sure I make the best possible disposition of them."<sup>31</sup>

Jefferson himself raised a few seedlings from Lewis' seeds, as he once informed McMahon:

"I shall be at home early in March for my permanent residence, and shall very much devote myself to my garden. I reserved very few of Governor Lewis's articles, and have growing only his salsafia, Mandane corn and a pea remarkable for its beautiful blossom and leaf. his forward bean is growing in my neighborhood."<sup>32</sup>

Two years later he sent to Dr. Barton, from these plants grown at Monticello, "some Ricara snap beans and Columbian salsafia brought from the western side of the continent by Captain Lewis."<sup>33</sup>

<sup>29</sup> Letter to Bernard McMahon, March 20, 1807 (14, LIX, No. 68).

<sup>30</sup> Letter to Bernard McMahon, March 22, 1807 (14, LIX, No. 69).

<sup>31</sup> Letter to Wm. Hamilton, March 22, 1807 (14, XLII, No. 26).

<sup>32</sup> Letter to Bernard McMahon, July 6, 1808 (14, LIX, No. 70).

<sup>33</sup> Letter to Dr. Benjamin S. Barton, October 6, 1810 (14, X, No. 81).

In February of 1812 McMahon sent Jefferson specimens of *Ribes odoratissimum*, *Symphoricarpos leucocarpa*, and a yellow currant, all found by Lewis, and eight months later Jefferson replied:

"The articles received in the spring . . . have been remarkably successful, one only of the cuttings of the snowberry failed. the rest are now very flourishing and shew some of the most beautiful berries I have ever seen. the sweet scented currant, the yellow currant, the red gooseberries and Hudson strawberries are all flourishing."<sup>34</sup>

It is also apparent, from other letters, that Jefferson was considerably irritated by delay in publication of the botanical and other scientific findings of the expedition. This delay was occasioned by preparation of engravings, by the tragic death of Lewis in 1809 and of Dr. Barton, by the outbreak of war with England in 1812, and by insolvency of the printers. In December, 1813, Jefferson expected Lewis' daily journal to appear soon in print, and on the basis of this expectation he wrote to his European friend, the explorer Baron Alexander von Humboldt:

"These I will take care to send you with the tobacco seed you desired, if it be possible for them to escape the thousand ships of our enemies spread over the ocean. The botanical and zoological discoveries of Lewis will probably experience greater delay, and become known to the world through other channels before that volume will be ready."<sup>35</sup>

To add to this exasperating delay, the original botanical and other scientific notes became dispersed among different persons who were reluctant to surrender them into one complete collection. By his persistent efforts, however, and with the assistance of the Abbé Corrêa de Serra and others, he finally succeeded in rescuing a considerable portion of the original notes and in getting them into the hands of a publisher, Paul Allen, as well as depositing them, on April 8, 1818, for safe keeping with the American Philosophical Society. It was not until 1904, however, one hundred years after Lewis and Clark started their famous trip, that their journals were published in full and as originally written. Jefferson was thus deprived of seeing the full consummation of his great project, but the pride which he took in its botanical findings is well exemplified by the following letter of his in 1813 to Madame de Tessé, a relative of the Marquis de la Fayette, who apparently had established some new gardens at Auenay in France:

"With the botanical riches which you mention to have been derived to England from New Holland, we are as yet unacquainted. Lewis's journey across our continent to the Pacific has added a number of new plants to our former stock. Some of them are curious, some ornamental, some useful, and some may by culture be made acceptable on our tables. I have growing, which I destine for you, a very handsome little shrub of the size of a currant bush.

<sup>34</sup> Letter to Bernard McMahon, October 11, 1812 (14, LXII, No. 125).

<sup>35</sup> Letter to Baron Alexander von Humboldt, December 6, 1813 (13 XIV, 20).

Its beauty consists in a great produce of berries of the size of currants, and literally as white as snow, which remain on the bush through the winter, after its leaves have fallen, and make it an object as singular as it is beautiful. We call it the snow-berry bush, no botanical name being yet given to it, but I do not know why we might not call it *Chionococcus*, or *Kallicoccus*. All Lewis's plants are growing in the garden of Mr. McMahon, a gardener of Philadelphia, to whom I consigned them, and from whom I shall have great pleasure when peace is restored [the war of 1812 was then raging], in ordering for you any of these or of our other indigenous plants.'<sup>36</sup>

In concluding this chapter it is only fair to note that Jefferson's concern for the determination of plants in botanical collections was not limited to material assembled by Lewis. A certain Mr. Dunbar, for instance, conducted an excursion up the Washita in the autumn and winter of 1804, and the following May Jefferson sent dried plant specimens from that journey to Dr. Barton for determination.<sup>36a</sup>

#### ACADEMIC CONCERN FOR BOTANY IN CURRICULA

That Jefferson appreciated the cultural value of botanical studies is apparent from many of his writings. In a letter from Paris, for instance, which he addressed in 1787 to his future son-in-law, Thomas M. Randolph, Jr., who at the time was studying at the University of Edinburgh, Jefferson advised, among other matters, that:

"Mathematics, Natural Philosophy, Natural History, Anatomy, Chemistry, Botany, will become amusements for your hours of relaxation and auxiliaries to your principal studies. Precious and delightful ones they will be. As soon as such a foundation is laid in them, as you may build on as you please hereafter, I suppose you will proceed to your main objects, Politics, Law, Rhetoric and History.'<sup>37</sup>

This observation is interesting not only in the thought contained in it, but because that thought was the direct converse of an idea which has long dominated in academic circles, even to very recent years, namely, that the so-called classics and cultural subjects should serve as a background for scientific pursuits. Many have been the embryonic and genuinely promising scientists who have wondered why they must delve into Greek, Latin, and perhaps ancient mythology, while students of the "classics" escaped the rigors of experimentation, analytic inquiry, and inductive reasoning. Perhaps Jefferson was a prophet here as elsewhere, for in the generations since him, the inherited awe for "classical" studies has very gradually relaxed in an increasing appreciation of the cultural values inherent in natural history.

<sup>36</sup> Letter to Madame de Tessé, December 8, 1813 (13, XIV, 25).

<sup>36a</sup> Two letters to Benjamin Smith Barton, May 2 & 21, 1805. (Library of Congress & Mass. Hist. Soc., according to citation No. 20.)

<sup>37</sup> Letter to Thomas Mann Randolph, July 6, 1787 (13, VI, 165).

Twenty years later, when Jefferson was President of the United States and that son-in-law had his own son of college age, Jefferson displayed the same concern for his grandson. To Dr. Caspar Wistar, prominent among the learned men who seemed to be concentrated in those days around Philadelphia, he was induced to write as follows:

"I have a grandson, the son of Mr. Randolph, now about fifteen years of age, in whose education I take a lively interest . . . I am not a friend to placing young men in populous cities, because they acquire there habits and partialities which do not contribute to the happiness of their after life. But there are particular branches of science, which are not so advantageously taught anywhere else in the United States as in Philadelphia. The garden at the Woodlands for Botany, Mr. Peale's Museum for Natural History, your Medical school for Anatomy, and the able professors in all of them, give advantages not to be found elsewhere. We propose, therefore, to send him to Philadelphia to attend the schools of Botany, Natural History, Anatomy, and perhaps Surgery; but not of Medicine."<sup>38</sup>

To the grandson's father he wrote as follows respecting this contemplated tutelage under Dr. Wistar:

"For a scientific man in a town nothing can furnish so convenient an amusement as chemistry, because it may be pursued in his cabinet; but for a country gentleman I know no source of amusement & health equal to botany & natural history, & I should think it unfortunate for such an one to attach himself to chemistry."<sup>39</sup>

To someone who disagreed with him he wrote:

"In the exclusion of Anatomy and Botany from the eleventh grade of education, which is that of the man of independent fortune, we separate in opinion. In my view, no knowledge can be more satisfactory to a man than that of his own frame, its parts, their functions and actions. And Botany I rank with the most valuable sciences, whether we consider its subjects as furnishing the principal subsistence of life to man and beast, delicious varieties for our tables, refreshments from our orchards, the adornments of our flower-borders, shade and perfume of our groves, materials for our buildings, or medicaments for our bodies. To the gentleman it is certainly more interesting than Mineralogy (which I by no means, however, undervalue), and is more at hand for his amusements; and to a country family it constitutes a great portion of their social entertainment. No country gentleman should be without what amuses every step he takes into his fields."<sup>40</sup>

It was only natural, therefore, that when the opportunity presented itself, Jefferson became instrumental in fostering botanical studies. That opportunity came after his retirement from the Presidency of the United States, when he was in a position to give sustained attention to the new university which he had long been planning to erect in Charlottesville near his home

<sup>38</sup> Letter to Dr. Caspar Wistar, June 21, 1807 (13, XI, 242).

<sup>39</sup> Letter to Thomas Mann Randolph, November 22, 1809 (18, 124).

<sup>40</sup> Letter to Dr. Thomas Cooper, October 7, 1814 (13, XIV, 199).

of Monticello. In writing to Joseph Priestley, the eminent English chemist, telling him of his plans for a university and soliciting his advice, Jefferson wrote:

"To you therefore we address our solicitations, and to lesson to you as much as possible the ambiguities of our object, I will venture even to sketch the sciences which seem useful and practicable for us, as they occur to me while holding my pen. Botany, chemistry, zoology, anatomy, surgery, medicine, natural philosophy, agriculture, mathematics, astronomy, geography, politics, commerce history, ethics, law, arts, fine arts."<sup>41</sup>

In 1803, as a result of Jefferson's endeavors, Albemarle Academy was founded. In 1817 it became Central College, and in 1825, in final consummation of Jefferson's long-cherished hope for a state university, the institution became the University of Virginia. It is particularly interesting to note that Jefferson had at one time hoped to place a botanist at the head of this institution, the Abbé José Francisco Corrêa da Serra.<sup>42</sup> This gentleman was a Portuguese politician, scholar and botanist who came to America in 1813 to prosecute researches in natural history, and who lectured for a time to the American savants gathered in Philadelphia when that city was the center of learning in the new republic. He had long been a friend of Jefferson, assisted him in planning the botany courses and garden at the University, and in 1816, instead of meeting Jefferson's wishes, became Portuguese Minister to the United States.

Constantine Samuel Rafinesque also entered into Jefferson's problems in connection with the set-up of the University. Like the two Michaux', he also was foreign-born and contributed much to early American botany. In 1819 he accepted a professorship in Transylvania University, Kentucky, but during the tenure of that office he was very anxious to become associated with Jefferson's new university. From correspondence between the two men (5) we learn that Rafinesque made repeated but vain overtures to Jefferson seeking his favor and courting an appointment from him to a position in the new institution. Jefferson appears not to have been particularly impressed by Rafinesque's qualifications, for his responses were rather equivocal, and before terminating his correspondence with Rafinesque, he sent a representative to Europe to engage professors for the University. As we shall soon note, it was a New Yorker who finally gained the coveted position.

It was also Jefferson's desire to have his university include a school of agriculture. The idea was not entirely new at that time, for nearly 20 years earlier he had also advocated establishing a school of agriculture in connection with his bold but vain suggestion to Washington that the great University of Geneva be bodily transferred from Switzerland to some place near

<sup>41</sup> Letter to Dr. Joseph Priestley, January 18, 1800 (13, X, 140).

<sup>42</sup> Letter to M. Dupont de Nemours, November 29, 1813 (13, XIX, 195).



the Federal city (Washington) in order that it might escape the Napoleonic scourge. Theodor de Saussure and Jean Senebrier were then associated with that institution, and in a few years they and Ingenhousz were destined to lay the foundations for a proper understanding of photosynthesis and respiration. In one of Jefferson's letters wherein he commented that

"The greatest evils of populous society have ever appeared to me to spring from the vicious distribution of its members among the occupations called for"

he also wrote:

"The class principally defective is that of agriculture. It is the first in utility, and ought to be the first in respect. The same artificial means which have been used to produce a competition in learning, may be equally successful in restoring agriculture to its primary dignity in the eyes of men. It is a science of the very first order. It counts among its handmaids the most respectable sciences, such as Chemistry, Natural Philosophy, Mechanics, Mathematics generally, Natural History, Botany. In every College and University, a professorship of agriculture, and the class of its students, might be honored as the first. Young men closing their academical education with this, as the crown of all other sciences, fascinated with its solid charms, and at a time when they are to choose an occupation, instead of crowding the other classes, would return to the farms of their fathers, their own, or those of others, and replenish and invigorate a calling, now languishing under contempt and oppression. The charitable schools, instead of storing their pupils with a lore which the present state of society does not call for, converted into schools of agriculture, might restore them to that branch qualified to enrich and honor themselves, and to increase the productions of the nation instead of consuming them."<sup>43</sup>

It must be borne in mind, when evaluating this comment, that Jefferson was not in favor of an industrialized America; he wanted it to develop primarily into an agricultural nation; his enthusiasm for agriculture, therefore, was not merely part of his broadness of mind but was an expression of the destiny, as he saw it, of his country. Others, however, did not share his convictions, and an agricultural school was not included in the University as finally founded, probably "because of the contempt felt by the votaries of higher classicism for so plebeian a pursuit" (30). Instead, a separate college of agriculture was founded at Blacksburg, Virginia.

The University did, however, acquire a school of natural history, headed by Dr. John P. Emmett of New York, who in his capacity of Professor was called upon to teach not only botany but also chemistry, geology, mineralogy, and zoology. Jefferson recommended in one of his last letters that Emmett give twelve dozen lectures per year, two dozen to botany and zoology, two dozen to mineralogy and geology, and eight dozen to chemistry.<sup>44</sup>

<sup>43</sup> Letter to David Williams, November 14, 1803 (13, X, 428).

<sup>44</sup> Letter to Dr. John P. Emmett, May 2, 1826 (13, XVI, 170).

Jefferson was also interested in establishing a botanical garden at the university but the idea never materialized. Emmett was primarily a chemist by training, and any preferences which he may have exercised toward test tubes and crucibles, together with the responsibility of teaching other physical sciences, postponed his developing the biological part of his curriculum. A year after his appointment botanical courses had apparently not yet been inaugurated, for Jefferson at that time found occasion to pen one of the last letters of his life in which he revealed once again his long-sustained interest in plant life, more particularly in revealing it to students. He wrote that letter on April 27, 1826, to Dr. Emmett. A little more than two months later he died. To quote this communication seems, therefore, a most appropriate means of concluding this tribute to the purely botanical interests of Thomas Jefferson:

"It is time to think of the introduction of the School of Botany into our institution. Not that I suppose the lectures can be begun in the present year, but that we may this year make the preparations necessary for commencing them the next. For that branch, I presume, can be taught advantageously only during the short season while nature is in general bloom, say during a certain portion of the months and April and May, when, suspending the other branches of your department, that of Botany may claim your exclusive attention. Of this, however, you are to be the judge, as well as of what I may now propose on the subject of preparation."

Jefferson then refers to several suggestions which he had solicited and received from the late Abbé Corrêa regarding the designs for a botanic garden. Six acres of land were available for the purpose. Flower-beds and an arboretum were to be instituted, but a greenhouse, owing to lack of funds, could not be considered. He then continues:

"1. Our first operation must be the selection of a piece of ground of proper soil and site, suppose of about six acres, as M. Corrêa proposes. In choosing this we are to regard the circumstances of soil, water, and distance. I have diligently examined all our grounds with this view, and think that that on the public road, at the upper corner of our possessions, where the stream issues from them, has more of the requisite qualities than any other spot we possess. . . .

"2. Operation. Enclose the ground with a serpentine brick wall seven feet high. This would take about 80,000 bricks, and cost \$800, and it must depend on our finances whether they will afford that immediately, or allow us, for awhile, but enclosure of posts and rails.

"3. Operation. Form all the hillsides into level terrasses of convenient breadth, curving with the hill, and the level ground into beds and alleys.

"4. Operation. Make a list of the plants thought necessary and sufficient for botanical purposes, and of the trees we propose to introduce, and take measures in time for procuring them.

As to the seeds of plants, much may be obtained from the gardeners of our own country. I have, moreover, a special resource. For three and twenty

years of the past twenty-five, my good friend Thouin, Superintendent of the Garden of Plants at Paris, has regularly sent me a box of seeds, of such exotics as to us, as would suit our climate, and containing nothing indigenous to our country. These I regularly sent to the public and private gardens of the other States, having as yet no employment for them here. But during the last two years this envoi has been intermitted, I know not why. I will immediately write and request a recommencement of that kind office, on the ground that we can now employ them ourselves. They can be here in the early spring.

The trees I should propose would be exotics of distinguished usefulness, and accommodated to our climate; such as the Larch, Cedar of Libanus, Cork Oak, the Marronnier, Mahogany, the Catachu (i.e., caoutchouc) or Indian rubber tree of Napul (30), Teak tree, or Indian oak of Burman (23), the various woods of Brazil, etc.

The seed of the Larch can be obtained from a tree at Monticello. Cones of the Cedar of Libanus are in most of our seed shops, but may be had fresh from the trees in the English gardens. The Marronnier and Cork Oak, I can obtain from France. There is a Marronnier at Mount Vernon, but it is a seedling, and not therefore select. The others may be got through the means of our ministers and consuls in the countries where they grow, or from the seed shops of England, where they may very possibly be found. Lastly, a gardener of sufficient skill must be obtained.

This, dear Sir, is the sum of what occurs to me at present; think of it, and let us at once enter on the operations."<sup>45</sup>

#### JEFFERSONIA

Jefferson was long associated with and at one time the third president of the American Philosophical Society, which revolved about the learned gentlemen who congregated in Philadelphia during the American colonial days. Among the members was Benjamin Smith Barton, professor of natural history, botany, and materia medica in Philadelphia College, which later became the University of Pennsylvania. It seems most fitting, in view of Jefferson's enduring interest in plants, that Dr. Barton and the Society, through their transactions of 1793 should have commemorated that interest by establishing a new genus of plants in his honor, *Jeffersonia*. In establishing the genus, Barton wrote:

"*Jeffersonia*, in honour of Thomas Jefferson, Esq., Secretary of State to the United States. I beg leave to observe to you, in this place, that in imposing upon this genus the name of Mr. Jefferson, I have had no reference to his political character, or to his reputation for general science, and literature. My business was with his knowledge of natural history. In the various departments of this science, but especially in botany and in zoology, the information of this gentlemen is equalled by that of few persons in the United States."<sup>46</sup>

<sup>45</sup> Letter to Dr. John P. Emmett, April 27, 1826 (13, XVI, 163).

<sup>46</sup> Trans. Am. Phil. Soc. 3: 342. 1793.

It is to be noted that this dedication was made before Jefferson distinguished himself in sponsoring the Lewis and Clark Expedition or urging agricultural and botanical studies. It was inspired, presumably, by his interest in agriculture and the introduction of new and valuable crop plants, by his gardening activities to be considered later, and by other considerations not revealed in his writings but undoubtedly well known to his contemporaries.

The genus thus established was monotypic at the time, and Barton named the one species *Jeffersonia binata*, the natural distribution of which today is known to extend from New York and Ontario to Wisconsin, Iowa, and Tennessee. Linnaeus, 40 years earlier, had named it *Podophyllum diphyllum*, and Persoon, after Barton, called it *Jeffersonia diphylla*, where it stands today. The plant is an herbaceous perennial of the Berberidaceae, popularly known as twin-leaf or rheumatism-root, and its rhizomes and roots have been used as adulterants and substitutes of those of *Aristolochia Serpentaria*, *A. reticulata*, and *Hydrastis canadensis*. The first two of these, known respectively as Virginia and Texas snakeroot, are the commercial sources of serpentaria, a pharmaceutical preparation of several alleged attributes but used principally in treatment of bronchitis and as an aromatic bitter. The dried rhizomes and roots of *Hydrastis* or goldenseal are used as alteratives to mucous membranes and as bitter tonics.

#### RESUMÉ

Jefferson's claim to fame in the realm of pure botany lies solely in the botanical aspects of two great projects which he conceived and executed, namely, the Lewis and Clark Expedition from St. Louis to the Pacific Coast, and the founding of the University of Virginia. Among the fruits of the former was a collection of plants, in the naming and preservation of which Jefferson was much concerned; and as part of the latter, he sponsored a school of botany which was established, and a botanical garden which never materialized. Outside his sponsorship of these two successful enterprises he contributed nothing by way of personally adding to the contemporary understanding of plants. That he was a profound admirer of plants and well acquainted with them is another matter, and in the next, third and last part of this series we shall consider the abundant and impressive evidence in that direction.

THE NEW YORK BOTANICAL GARDEN  
NEW YORK

THE GENUS *JATROPHA* IN AMERICA: PRINCIPAL  
INTRAGENERIC GROUPS

ROGERS McVAUGH

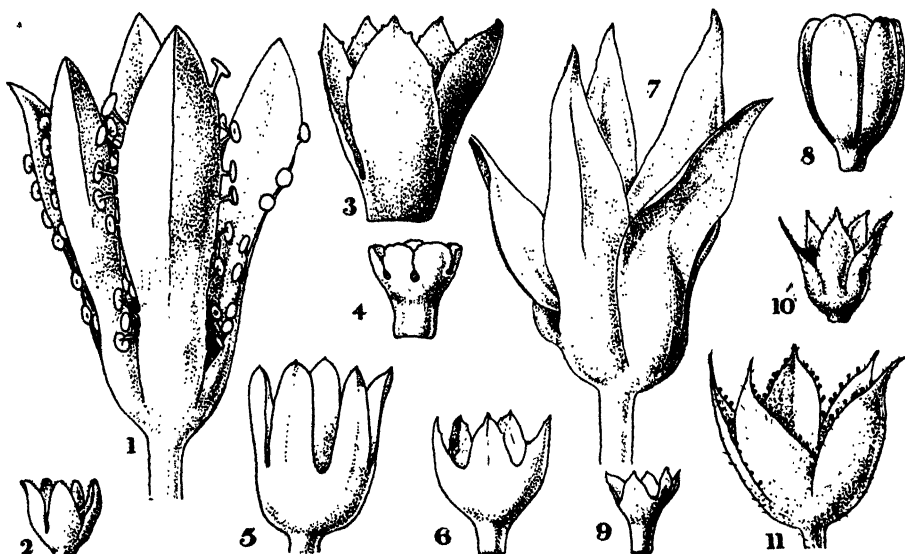
The euphorbiaceous genus *Jatropha* comprises perhaps 125 species, most of which are American or African; probably 40-50 species are African and about 75 American; a few are natives of Arabia or the southern Indian region. The closest affinities of the genus appear to be with *Manihot* and *Cnidoscolus*; it has likewise considerable apparent affinity with *Aleurites* and with *Hevea*, but these latter genera are usually referred to another tribe on the basis of technical characters of calyx aestivation. Several species of *Jatropha*, originally American, have become widely dispersed in the tropics because of their cultivation for ornament, for shade trees or for medicinal purposes, and at least a few species of the genus are familiar to many botanists and collectors, so that the name *Jatropha* is a familiar one in botanical literature. At least one species, *J. Curcas*, has attained much notoriety as a common poisonous plant of the tropics, and more lately has been thought of as a possible source of a drying oil similar to tung oil. Botanically the genus has received its share of attention, with the usual concomitant duplication of names for species and other subgeneric groups, and misapplication of names; as in any generic group of similar size, new entities have been discovered from time to time since the publication of the last treatment of the genus as a whole, and a modern synopsis of all the American species would be of value to working systematists. As a step preliminary to this, the present paper attempts to set forth what appear to be the principal lines of divergence within the genus; at the present time it is impracticable to prepare a detailed synopsis of all species, chiefly because so many are poorly known. For example, to consider the situation in North America alone, at the time of publication of Standley's *Trees and Shrubs of Mexico* (1923) its author included 19 distinct and well-marked species of *Jatropha* (excluding *Cnidoscolus*); 6 of these were scarcely or not at all known except from the type, and not more than 8 were represented in herbaria by enough material to give a fair idea of the species. Since 1923 about 8 species have been added to the known flora of Mexico, 7 of which are known from the type only or from very scanty material.

## SUMMARY OF PREVIOUS CLASSIFICATION OF THE GENUS

Detailed taxonomic studies of *Jatropha* have been two: The genus was written up by Mueller for the DeCandolle *Prodromus* (1866) and by Pax

for *Das Pflanzenreich* (1910). Both these authors included in *Jatropha* the species with stinging hairs and a single floral envelope, the group long before segregated by Pohl as a genus, *Cnidoscolus*. I have set forth elsewhere my reasons for maintaining the latter as distinct from *Jatropha* (McVaugh 1944).

Mueller divided *Jatropha* into three sections, making *Cnidoscolus* equal in rank to the others, *Adenorhopium* and *Curcas*. It now appears that although his major divisions were well founded, the two latter sections are much more closely related to one another than to *Cnidoscolus*. *Adenorhopium*



Calyces of *Jatropha*, 5 times natural size. FIG. 1. *Jatropha cordata*, ♀, Gentry 2275, Sonora. FIG. 2. *J. cordata*, ♂, Gentry 2274, Sonora. FIG. 3. *J. macrantha*, ♂, Balls 5878, Peru. FIG. 4. *J. Humboldtiana*, ♂, Weberbauer 6211, Peru. FIG. 5. *J. integerrima*, ♀, Fennell 462, from cultivation. FIG. 6. *J. integerrima*, ♂, Lundell 1597, Petén. FIG. 7. *J. Curcas*, ♀, Pittier 2400, Panama. FIG. 8. *J. Curcas* var. *rufus*, ♂, Ortega 7299, Sinaloa. FIG. 9. *J. ocharctica*, ♂, Texas. FIG. 10. *J. excisa*, ♂, Venturi 7991, Argentina. FIG. 11. *J. excisa*, ♀, Venturi 7991.

and *Curcas*, indeed, are separable with some difficulty, the sectional lines having in the past been drawn chiefly upon a single character, the degree of coherence of the petals of the pistillate flower.<sup>1</sup> In his division of the genus Mueller was followed closely by Pax, who used the same criteria for delimitation of the groups, which he considered subgenera ("Untergattungen") rather than sections.

Mueller's treatment of *Jatropha* was rather strongly influenced by the previous work of Baillon (1858), who had proposed to take up Adanson's

<sup>1</sup> DC. Prodr. 15(2): 1076. 1866. "[Sect. *Curcas*] a sect. *Adenorhopio* vix nisi petalis florum foem. arctissime cohaerentibus differt."

genus *Curcas* for those species having a gamopetalous corolla, and to restrict the use of the name *Jatropha* to the polypetalous species. Baillon's genus *Jatropha* thus included *Adenoropium* of Pohl as an exact synonym, but while Pohl had segregated the species of *Adenoropium* from *Jatropha* chiefly on the basis of the abundant foliar and other glands of the species known to him, Baillon relied upon the corolla-character. Many of the species accepted by Baillon as polypetalous are not so, and the character is at best of doubtful value in classification in this group. Whatever the wisdom of his course, however, Baillon's ideas on the relationships of species seem to have been accepted by Grisebach, (1864, p. 36) who assigned *J. gossypifolia*, *J. multifida*, *J. hastata* Jacq., and *J. divaricata* Sw. to a new section, *Adenorhopium*<sup>2</sup> (subsequently taken up by Mueller) which he described as having "Petals distinct, or cohering at the base." Grisebach's second section, *Curcas*, included *J. hernandifolia* Vent., and *J. Curcas*, and was apparently based on Baillon's conception of the genus *Curcas*, for it is described as having the "Corolla sympetalous."

The above arrangement of the genus, based on the single corolla-character, is actually somewhat too simple to be a natural one. All the American species known to me, however, may be separated into four principal groups, each of which is more homogeneous than either of the great sections accepted by most authors. Of these four one is chiefly Mexican, one Antillean, one Andean, and one appears to be best developed in the south-Brazilian—Paraguayan region. They may be distinguished as follows:

1. Calyx in both staminate and pistillate flowers scarious or subherbaceous, the pistillate sometimes larger but not conspicuously different otherwise from the staminate; calyx-lobes little or not at all imbricated at anthesis, often separated by broad rounded sinuses; petals distinct or essentially so, scarlet to vermilion . . . . . 2.
2. Petals hirsute within at base; style-tips slender, margined and hooded by the stigmatic surfaces; stamens 10, the anthers sagittate, at least the inner ones strongly curved . . . . . Sect. *Polymorphae* Pax.
2. Petals glabrous; style-branches with fleshy capitate stigmatic tips; stamens 8, the anthers usually long-linear, erect . . . . . Sect. *Macranthae* Pax.
1. Calyx of the pistillate flowers usually definitely herbaceous, usually larger than and often conspicuously different from that of the staminate, which may be herbaceous or scarious; calyx-lobes usually imbricate even until anthesis, the sinuses very narrow; corolla definitely tubular (usually at least a third its length), campanulate to cylindric, variously colored but rarely bright red as in no. 1, above . . . . . 3.
3. Calyx in both sexes herbaceous, the lobes usually glandular-margined; plants monoecious, usually with many small glands on leaf-margins,

<sup>2</sup> This spelling is that used by Grisebach and is etymologically correct, but is not that used by Pohl, although Grisebach doubtless intended to base his section upon Pohl's genus. Since Grisebach made no mention of Pohl's work, there would appear to be no justification for citing the name of the latter as a parenthetical authority for the sectional name, regardless of the essential identity of the two groups and the probable intentions of the later author.

bracts and stipules; stamens usually 8, the anthers short and broad; corolla purple to purple-red or yellow, the tube usually shorter than the lobes; seeds with small scar and large fimbriate caruncle ... Sect. *Adenorhopium* Griseb.

3. Pistillate calyx usually herbaceous, the lobes sometimes glandular-margined; staminate calyx quite different in aspect, more or less scarious, the lobes usually entire; plants (sometimes monoecious) usually polygamous or dioecious; most species not or but sparsely glandular; stamens usually 10, the anthers short and broad; corolla green or yellow to white, pink, or sometimes red, the tube usually longer than the lobes; seeds (often rounded) mostly with a broad irregular scar and a small caruncle.

Sect. *Mozinna* (Ortega) Pax.

1. Sect. **POLYMORPHAE** Pax, Pflanzenreich IV. **147**: 48, emend. 1910.

*Jatropha*, subgen. *Adenoropium*, sect. *Polymorphae* Pax, l.c., as to type species.

The plants of this section are shrubs or trees with sticky watery sap (according to Jacquin) and small pith. The leaves are palmately veined (or in entire or subentire forms pinnately veined except for the two strong ascending basal veins); blades often with a few glandular teeth, especially near base; stipules small, subulate, and entire; inflorescence corymbose, the lower branches alternate; petals distinct, bright red, 10–15 mm. long, narrowed to a very short claw; calyx campanulate, with blunt lobes which are entire or few-toothed, scarcely imbricate even in bud; stamens 10 in 2 whorls; styles 3, deeply cleft into two filiform hooded tips; glands 5, free; fruits small, dry; seeds oblong, with reflexed and lacerate caruncle and small hilum.

LECTOTYPE-SPECIES. *Jatropha integerrima* Jacq.

Pax included here 8 Cuban and 5 African and Arabian species; material of the Old World species [*J. unicostata* Balf. f., *J. variegata* (Forsk.) Vahl, *J. capensis* (L. f.) Sond., *J. variifolia* Pax, and *J. prunifolia* Pax] has not been available for study, but all appear from descriptions to agree in having 8 (not 10) stamens, and most are said to have lobed or dissected stipules and greenish or yellowish (not red) petals, so their relationships to the Cuban species are probably not close. The use of the name *Polymorphae* may accordingly be restricted to the Cuban species, the disposition of the Old World species being left for the future.

This group is, so far as known, restricted to the Greater Antilles except as found in cultivation elsewhere in the tropics and occasionally established; the species are probably all originally natives of Cuba only. The described species number about 12; in 1910 Pax recognized but 8, admitting at the same time that *J. panduraefolia*, *J. integerrima*, *J. hastata*, *J. glaucovirens*, and *J. pauciflora* were inseparable except by leaf-characters. Actually there seem to be not more than three or four species, including *J. angustifolia* Griseb., *J. tupifolia* Griseb., *J. Paxii* Croiz., and the group of *J. integerrima* Jacq.; the latter is an extremely variable species (as to form of leaves), long cultivated in Cuba under the name of "peregrina," and many times described botanically. I am referring to this species, as synonyms, *J. hastata* Jacq., *J. acuminata* Desr., *J. panduraefolia* Andr., *J. diversifolia* A. Rich.,

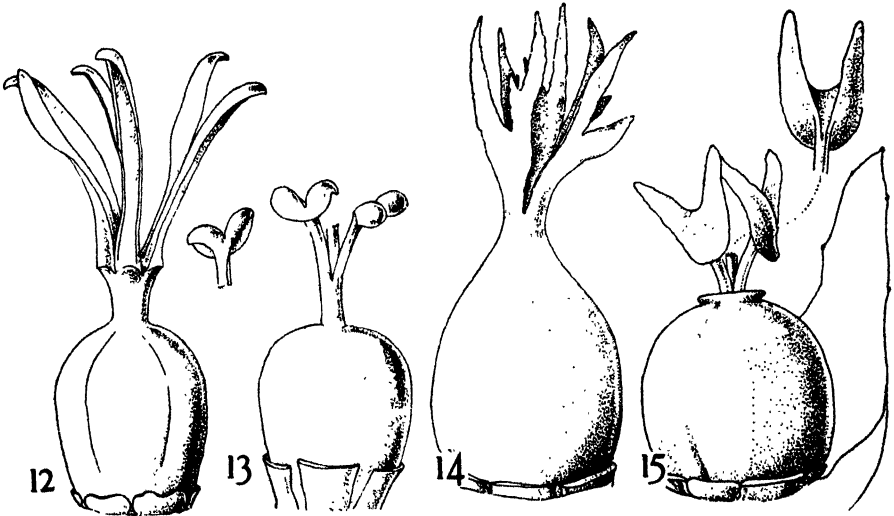


*J. moluensis* Sessé & Moc., *J. glaucovirens* Pax & Hoffm., and *J. pauciflora* Griseb. *Jatropha minor* Urb., said to be related to *J. tupidifolia*, is unknown to me. Apparently *J. hastata* Jacq. and *J. integerrima* Jacq., the earliest (and simultaneously published) names for this species, have never before been combined under the one name or the other, although they have been combined several times under other names, especially under *J. diversifolia*, which was originally published to include both, and under *J. panduraefolia*.

2. Sect. MACRANTHAE Pax, Pflanzenreich IV. 147: 46, emend. 1910.

*Jatropha* subgen. *Adenoropium*, sect. *Macranthae* Pax, i.e. as to type; sect. *Glanduliferae*, subsect. *Lobatae* Pax, op. cit. 31, pars; subsect. *Pubescentes* Pax, op. cit. 37, pars; subsect. *Multifidae* Pax, op. cit. 40, pars; subsect. *Peltatae* Pax, op. cit. 43; subgen. *Curcas*, sect. *Mozinna*, subsect. *Mutabiles* Pax, op. cit. 83.

Monoecious shrubs or small trees, or fleshy herbs with stout woody bases, often with peltate or subpeltate leaves; stipules various, often dissected and



Pistils of *Jatropha*, 10 times natural size. FIG. 12. *J. integerrima*, Fennell 462. FIG. 13. *J. gossypifolia*, Orcutt 3407, Mexico. FIG. 14. *J. Gaumeri*, from the type. FIG. 15. *J. macrantha*, Balls 5878, Peru.

glandular, and sometimes persistent and indurated; inflorescence mostly corymbose, pedunculate, the lower branch or branches of the cyme alternate; petals large and showy (mostly 1–1.5 cm. long), distinct or essentially so, usually glabrous, scarlet or vermillion to yellow; calyx more or less scarious and nearly smooth in flowers of both sexes, the lobes often short and blunt, usually little or not at all imbricate except in bud, the tube often relatively long; stamens usually 8 (5 in the outer whorl), the anthers elongate, linear, sagittate; styles 2-cleft, mostly slender and elongate, the stigmas capitate or horseshoe-shaped, fungoid-fleshy; floral glands distinct or in some species truly annular; seeds with small scar and large fimbriate caruncle.

TYPE-SPECIES, *Jatropha macrantha* Muell. Arg.

Species of this section are readily to be separated from those of sect. *Adenorhopium* by the corolla characters, the elongate anthers, the tendency of the calyx to become scarious, and the relative lack of stipitate glands (most species of *Adenorhopium* have copious glands on the petioles, along the leaf-margins and on the calyx).

All the species now assigned to sect. *Macranthae* (except *Jatropha mutabilis*) were originally placed by Pax in his subgenus *Adenoropium*, but the section as originally constituted was a heterogeneous one of 5 species with little in common, set off by Pax on the basis of their much-reduced stipules. The original species of the section were *J. ciliata* Muell. Arg., *J. macrocarpa* Griseb., *J. macrantha* Muell. Arg., *J. pachypoda* Pax. and *J. Andrieuxii* Muell. Arg. Subsequently described species to be added to the narrowly circumscribed section are *J. Augusti* Pax & Hoffm., *J. Hoffmanniae* Croiz. (*J. longipedunculata* Pax & Hoffm.), *J. multiflora* Pax & Hoffm., and *J. papyrifera* Pax & Hoffm.

Mueller (1866) recognized the homogeneity of the group *Macranthae* (in the present enlarged sense), and grouped the nine species known to him into one of the six divisions of his section *Adenorhopium*; the only exception to this was *J. macrantha*, of which he had incomplete material, and which he set up in a distinct group.

In contrast to Mueller, Pax distributed the 11 species known to him in 1910 (excluding those placed by him in *Macranthae*) among 4 subsections of his section *Glanduliferae*, and set up for *J. mutabilis*, which was unknown to Mueller, a monotypic subsection in his subgenus *Curcas*. Pax's disposition of the species was as follows: Subsection *Lobatae* (*J. ricinifolia* Pax, *J. Hieronymi* Kuntze, *J. Weddelliana* Baill.); Pubescentes [*J. Martiusii* (Pohl) Baill., *J. Pohliana* Muell. Arg.]; Multifidae (*J. multifida* L., *J. Berlandieri* Torr.); *Peltatae* (*J. peltata* H.B.K., *J. podagrica* Hook., *J. Weberbaueri* Pax & Hoffm., *J. nudicaulis* Benth.). The subsequently described *J. grossidentata* Pax & Hoffm. is said to be closely related to *J. Weddelliana*.

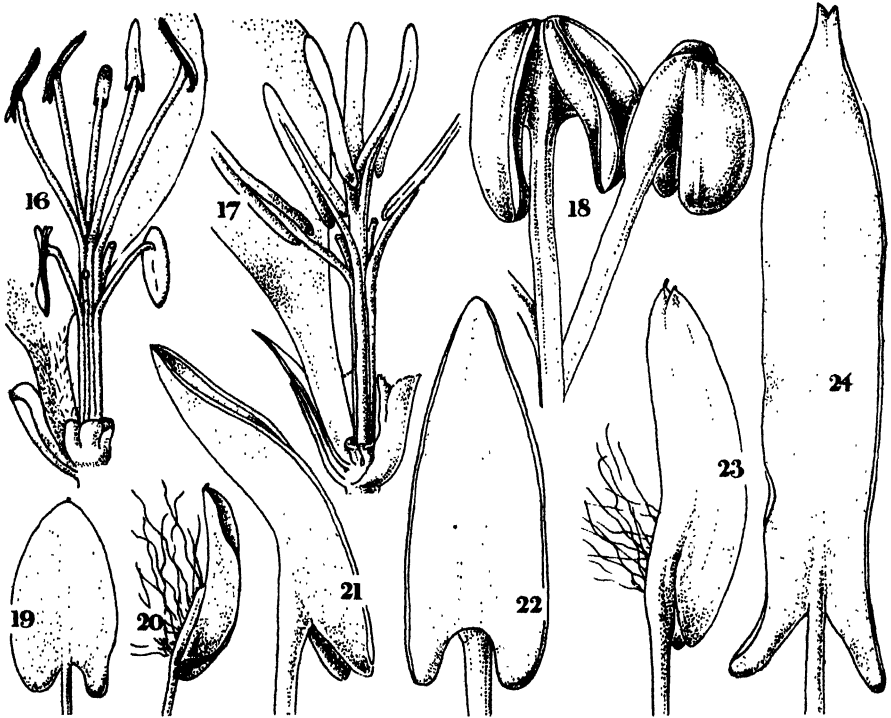
The subsections constituted by Pax were distinguished almost wholly on gross characters of the leaves (degree of lobing, amount of pubescence, etc.), but it seems that a better idea of relationships may be obtained by study of the floral structures of these species with variable leaves, so that (African species excluded) I should leave intact but one of Pax's subsections of his sect. *Glanduliferae*, namely subsect. *Adenophorae*, which he based chiefly upon the glandular petioles of the included species. The above species, with those from sect. *Macranthae* as understood by Pax, may then be disposed of as follows:

1. Shrub with leaves rounded, small, entire or denticulate, to 3.5 cm. long, on petioles 5 mm. long or less; calyx-lobes thickly glandular-margined, pubescent, not scarious; stipules minute, subulate, deciduous; stamens 8; eastern Brazil (Bahia, Alagoas) ..... *J. mutabilis* (Pohl) Baill.

1. Leaves various, usually at least 10 cm. broad, variously lobed and toothed, long-petiolate ..... 2.
2. Stipules reduced to sessile glands or minute and indurated ..... 3.
3. Leaf-margins glandular-serrate or glandular-denticulate ..... 4.
4. Leaves with shallow triangular lobes; stamens 8 (or 9); southern Peru ..... *J. ciliata*, *J. Augusti*, *J. Hoffmanniae*.
4. Leaves divided nearly to base into elliptic lobes; stamens unknown; plants (¶always) dioecious, with 5 carpels; Bolivia ..... *J. pachypoda*.
3. Leaves deeply 3- or 5-lobed, the margins of the lobes entire; carpels 3; stamens 10 ..... 5.
5. Leaves usually 3-lobed; inflorescence corymbose, congested, few-flowered; corolla scarlet; Atlantic slope of northern Peru ..... *J. macrantha*.
5. Leaves usually 5-lobed; inflorescence much elongated (to 20-30 cm.) and many-flowered, falsely racemose, bearing short lateral cymes; corolla red and yellow or orange (or white); northern Argentina and Bolivia ..... *J. macrocarpa*, *J. papyrifera*.
2. Stipules setaceous-dissected, usually gland-tipped, often persistent ..... 6.
6. Leaves definitely peltate; stamens 8 ..... 7.
7. Leaf-margins ciliate with slender stalked glands; northern Amazonian Peru ..... *J. Humboldtiana* McVaugh (*J. peltata* H.B.K.).
7. Margins of lobes entire or dentate, sometimes apiculate, not glandular-ciliate ..... 8.
8. Stipules indurate, the persistent woody bases antler-like; margins of lobes entire ..... 9.
9. Stipules glabrous; floral gland annular; calyx-lobes roundish, nearly entire, about 1.5 mm. long; corolla-lobes up to 8 mm. long; Central America and in cultivation ..... *J. podagrica*.
9. [Stipules with long matted deciduous hairs; floral glands distinct; calyx-lobes (pistillate) acuminate; corolla 10 mm. long; Colombia and Ecuador, not seen] ..... *J. nudicaulis*.
8. Stipules delicate, not indurated at base; margins of lobes entire or with few large teeth; Amazonian Peru ..... *J. Weberbaueri*.
6. Leaves not peltate, deeply palmately divided ..... 10.
10. Leaves with (5) 7-13 narrow divisions, these usually irregularly and coarsely lobulate, rarely entire, never regularly denticulate ..... 11.
11. Stem herbaceous, to about 0.3 m. high; stipules 2-3 mm. long, bifid or trifid; Texas and northern Mexico. .... *J. cathartica* Ter. & Berl. (*J. Berlandieri*).
11. Shrub or small tree to 6 or 7 m. high; stipules 1-2 cm. long, much dissected; tropical America; much in cultivation ..... *J. multifida*.
10. Leaves palmately 3- to 5- (7-) lobed, the lobes toothed or entire, never irregularly lobulate ..... 12.
12. Leaf-margins serrulate, dentate or ciliate-denticulate, the teeth not gland-tipped; stamens 8; carpels 3; eastern Brazil to northern Argentina. .... *J. Weddelliana*, *J. Hieronymi*, *J. ricinifolia*, *J. Martiusii*, *J. mollissima* (Pohl) Baill. [*J. Pohlana*], *J. grossidentata*.
12. Leaf-margins glandular-serrulate; stamens 10 (¶always); carpels 5 (¶always); Bolivia ..... *J. pachypoda*, *J. papyrifera*.

*Jatropha Robertii* S. Moore, from Corumbá, Brazil, is unknown to me, but evidently belongs to *Macranthae*, as the stamens are said to be 8 in num-

ber, and the petals pink and distinct; the stipules are unknown and the leaf-margins are entire or undulate. *J. Andrieuxii*, assigned by Pax to sect. *Macranthae*, certainly belongs with the other Mexican species of *Mozinna*. As indicated above, I should transfer *J. mutabilis* from *Mozinna* to *Macranthae*, for its flowers, except for the hairy glandular calyx-lobes, are exactly typical of the latter section; Pax seems to have erected the subsection *Muta-*



Androecia (5 times natural size) and anthers (25 times natural size) of *Jatropha*. FIG. 16. *J. integerrima*, Mo. Bot. Gard. no. 266/04/47, Thompson 95, from cultivation. FIG. 17. *J. ciliata* Muell. Arg., Herrera 3053, Peru. FIG. 18. Anthers of *J. gossypifolia*, Steere 1759, Campeche. FIG. 19. Outer (lower) anther, ventral (outer) face, *J. plataniifolia*, from an isotype. FIG. 20. Inner anther, lateral view, of the same. FIG. 21. Inner anther, lateral view, *J. integerrima*, Thompson 95. FIG. 22. Same, ventral face. FIG. 23. Inner anther, lateral view, *J. Curcas*, Popenoe 395, from cultivation. FIG. 24. Inner anther, ventral face, *J. ciliata* Muell. Arg., Stork et al. 10530, Peru.

Most of the drawings were made by Mr. B. Y. Morrison, from my sketches and notes.

biles wholly upon the superficial similarity between the leaves and twigs of *J. mutabilis* and those of several Mexican species of *Mozinna*.

It will be noted that no attempt has been made, in the key, to separate *J. ciliata* Muell. Arg. from the species supposedly related to it; the material at my disposal is entirely inadequate for the revision of this small group, but it appears that *J. Augusti* Pax & Hoffm. will have to be taken up for *J.*

*ciliata*, which is preoccupied by *J. ciliata* Sessé. The species of the group including *J. Weddelliana*, *J. mollissima* and *J. ricinifolia* are separated by Pax on the basis of pubescence alone and further study may show the number of species to be somewhat less than now supposed. The name *J. Pohliana*, used by Mueller and Pax, must be supplanted by one of the names proposed earlier by Pohl, and *J. mollissima* seems most suitable. *Jatropha pachypoda* is unknown to me except from a photograph of the type (*Fiebrig 3040a*, Field Mus. neg. 5396); this plant bears a strong superficial resemblance to *J. mollissima* and its relatives, suggesting the necessity of a careful study of additional material to determine the actual number of stamens and carpels normal for the species.

I have not attempted to subdivide the *Macranthae* into subsections, but on the basis of floral characters and those of the inflorescence, respectively, the aberrant species appear to be *J. macrantha* and *J. macrocarpa*.

### 3. Sect. ADENORHOPIUM Griseb. Fl. Br. W. Ind. 36, emend. 1864.

*Adenoropium* Pohl, Pl. Bras. Ic. 1: 12, pl. 9, as to type species. 1827; *Jatropha*, untergatt. *Adenoropium* (Pohl) Pax, Natürl. Pflanzenfam. 3(5): 75, as to type species. 1890; subgen. *Adenoropium*, sect. *Glanduliferae*, subsect. *Adenophorae* Pax, Pflanzenreich IV. 147: 25, in clavi. 1910; subsect. *Purpureae* Pax, op. cit. 26; sect. *Tuberosae*, subsect. *Latifoliae* Pax, op. cit. 60, in clavi (pars); subsect. *Macrorrhizae* Pax, op. cit. 61, pars.

Monoecious shrubs or herbs with glandular herbage, the leaf-margins, calyx-lobes, stipules and usually the petioles beset with stipitate glands; stipules dissected and glandular; inflorescence corymbose, the lowest branch or branches alternate; corolla relatively small (mostly less than 1 cm. long) definitely tubular, the segments loosely coherent one-third to one-half their length, mostly entirely glabrous, in color purplish-red to yellow, often with a pale tube; calyx usually herbaceous in flowers of both sexes, usually pubescent, with imbricate lobes; stamens usually 8, the anthers short, the inner three in many species with divergent sacs; styles 2-cleft, often short (?), the stigmas capitate or horseshoe-shaped, fungoid-fleshy; floral glands distinct; seeds with small scar and large fimbriate caruncle.

TYPE-SPECIES, *Jatropha gossypifolia* L.

Most if not all the African and Arabian species appear to belong to this section, having 8 stamens, yellow to purple corolla, glandular foliage, divided or reduced stipules and a lacerate or fimbriate caruncle; definite disposition of the Old World species must await further study.

The American species of *Adenorhopium* include several closely related South American species and two aberrant North American species; these may be arranged as follows:

1. Leaves more or less incised-serrate, at least the tips of the lobes with spinulose teeth, the margins not glandular; calyx somewhat scarious, the lobes long and narrow, fimbriate-toothed, not glandular; stamens 10; southwestern United States and northwestern Mexico ..... *J. macrorrhiza* Benth.

1. Plants with glandular herbage, the leaf-margins and calyx-lobes not as above; stamens 8 or 10 ..... 2.
2. Leaves slender-petiolate, glabrous, the petioles eglandular, the blades small, up to about 3.5 cm. long, truncate at base, hastately 3-lobed with the middle lobe narrow, caudate or acuminate; Sinaloa and Sonora ... *J. purpurea* Rose.
2. Leaves elliptic to ovate and unlobed, nearly sessile, or palmately parted or lobed, then with slender glanduliferous petioles; stamens 8-10 ..... 3.
3. Leaves broadly elliptic or rounded to ovate, neither lobed nor divided, essentially entire and usually glabrous except for the densely glandular-ciliate margins; petioles 3-6 mm. long or less; stamens 8(-10); southeastern Brazil, Paraguay, northern Argentina and eastern Bolivia ..... *J. eglandulosa* Pax,  
*J. elliptica* (Pohl) Muell. Arg., *J. intermedia* (Chod. & Hassl.) Pax,  
*J. Isabelli* Muell. Arg. and var. *antisiphilitica* (Speg.) Pax,  
*J. puncticulata* Pax & Hoffm., *J. rigidifolia* Pax & Hoffm.
3. Leaves more or less palmately lobed (or on some plants partly unlobed), usually with definite slender glanduliferous petioles; stamens 8-10 ..... 4.
4. Stems herbaceous, simple or sparsely branched; petioles much shorter than the blades, mostly 1-2(4) cm. long; inflorescence few-flowered, compact, usually not surpassing the leaves; Paraguay and adjacent Brazil and Argentina.  
*J. Isabelli* Muell. Arg. (?), *J. dissecta* (Chod. & Hassl.) Pax,  
*J. rigidifolia* Pax & Hoffm., *J. brachypoda* Pax, *J. induta* (Chod. & Hassl.) Pax, *J. transiens* Pax.
4. Stems usually definitely shrubby, copiously branched; petioles usually elongated and about equalling the blades, often 4-8(12) cm. long; inflorescence often surpassing the leaves, the main axis and lower branches often elongated ..... 5.
5. Petioles with expanded foliaceous margins, the margins glandular; northwestern Argentina ..... *J. Peiranoi* Lourt. & O'Don.
5. Petioles not foliaceous-margined ..... 6.
6. Leaves not lobed as deeply as to the middle of the blade; Paraguay and adjacent Brazil and Argentina ..... 7.
7. Staminate sepals entire.  
*J. Katharinae* Pax, *J. ribifolia* (Pohl) Baill.
7. Staminate sepals glandular-ciliate.  
*J. guaranítica* Speg., *J. Bornmülleri* Pax,  
*J. breviloba* (Morong) Pax & Hoffm.
6. Leaves lobed to the middle of the blade or (usually) more deeply ..... 8.
8. Inflorescence usually many-flowered, elongated, much exceeding the leaves, its lateral branches alternate, loosely flowered; stamens (always) 10; petiolar glands simple and sparingly branched on the same leaf; Bolivia, northern Argentina and Paraguay.  
*J. excisa* Griseb., *J. flavovirens* Pax & Hoffm.,  
*J. thyrsantha* Pax & Hoffm.
8. Inflorescence few-flowered or if many-flowered the lateral branches bearing small dense flower-clusters; flowers usually not much if at all exceeding the leaves; stamens 8(or 10); petiolar glands various ..... 9.
9. Petiolar glands simple, clavate; leaves deeply parted; Bolivia ..... *J. clavuligera* Muell. Arg.

9. Petiolar glands predominantly several-branched, sometimes a few simple.

*J. gossypifolia* L., *J. pedatipartita* Kuntze,  
*J. intercedens* Pax, *J. hippocastanifolia* Croiz.,  
*J. malmeana* Pax & Hoffm., *J. tacumbensis* Pax & Hoffm.

*Jatropha macrorrhiza* is here assigned to sect. *Adenorhopium* on the basis of its tubular corolla, its dissected stipules and its fimbriate caruncle, although it seems to have no close relatives in the genus (in any section) and lacks the characteristic glands of *Adenorhopium*. *Jatropha purpurea* likewise differs markedly from the remaining members of the section, and perhaps should be assigned to a distinct subsection, as Pax proposed. These two species excepted, the section *Adenorhopium* as here delimited is an exceedingly homogeneous one, easily condensed by a not-too-conservative systematist into about four species; more than 30 species, however, have been proposed, more than half of them by Pax or by Pax and Hoffmann. Most of these latter have been based principally upon leaf-, sepal- and indument-characters.

The American species which I should refer to sect. *Adenorhopium* (except *J. macrorrhiza* and *J. purpurea*) were assigned by Pax either to his sect. *Glanduliferae* subsection *Adenophorae*, characterized by its glanduliferous petioles in combination with a shrubby habit, or to sect. *Tuberosae*, subsect. *Latifoliae* (plants with herbaceous habit and elliptic unlobed leaves: *J. elliptica* and related species) or subsect. *Macrorrhizae* (plants with herbaceous habit and lobed or unlobed leaves: *J. dissecta* and *J. Isabelli*). These differences seem hardly great enough to constitute the principal bases for intra-generic divisions, but nevertheless amply distinguish small groups of related species.

I have not attempted to distinguish in the above key between *J. elliptica* and its supposed relatives, the types being unavailable and the stated differences between species being almost wholly minor ones. Pax supposed *J. Isabelli* to be closely akin to *J. dissecta*, apparently because of the predominantly herbaceous nature of both species; he proposed *J. induta*, *J. transiens* and *J. brachypoda* as "subspecies" or "formae intermediae," supposing them to be of the nature of hybrids between *J. Isabelli* and *J. dissecta*. A photograph of the type of *J. Isabelli*, however, suggests that it may be most closely related to the group of *J. elliptica*, having normally unlobed leaves, than to the group with deeply parted leaves and short petioles including *J. dissecta*, and specific limits in this latter group must remain to be worked out. Another group of this affinity, that having the leaf-blades shallowly lobed (*J. ribifolia*, etc.), is likewise a Paraguayan assemblage in which specific limits remain to be clarified. The fourth species-group which seems naturally distinct is that including *J. excisa* and probably *J. thyrsantha* and *J. flavovirens*; plants of this affinity seem to be most numerous in northern Argentina and adjacent areas, and are set off from all others by the loose

inflorescence, the mostly simple petiolar glands and (in all specimens I have examined) the 10 stamens. Finally there remain *J. gossypifolia* and the species I take to be its immediate relatives; again final disposition of these must await examination of the types and study of more extensive series of specimens than are now available in this country. *Jatropha clavuligera* is supposedly distinct because of the simple petiolar glands and deeply parted leaves, but other material from the same region (the Bolivian highlands), including the type collection of *Jatropha pedatipartita*, has the same leaf-shape and a similar inflorescence and similar pubescence, but has the petiolar glands both simple and branched on the same leaf. It seems probable that the type of *J. clavuligera* was an aberrant individual which bore simple glands only or which had lost the branched ones before Mueller examined it.

4. Sect. MOZINNA (Ortega) Pax. Natürl. Pflanzenfam. 3(5) : 75. 1890.

*Mozinna* Ortega, Pl. Dec. 8: 104, as genus. 27 Ja., 1799; *Curcas*, sect. *Mozinna* (Ortega) Baill. Etud. Gen. Euphorb. 315. 1858.

Shrubs or small trees, monoecious or (often) dioecious; stipules usually very small; staminate inflorescence slender, many-flowered, several times dichotomous; pistillate inflorescence reduced, stout, 1-3-flowered; bracts and sepals of the staminate flowers more or less scarious, usually entire and non-glandular, not herbaceous; sepals of the pistillate flowers larger, usually herbaceous, often toothed or glandular; corolla of both sexes cylindric-urceolate with recurved lobes, the tube usually longer than the lobes, more or less hirsute within at base; stamens regularly 10, the anthers ovate to linear but if slender then relatively short, often 1 mm. long or less; locules of the ovary and primary style-branches (normally 3) often reduced to 2 or 1; primary style-branches once bifurcate, with thickened fungoid stigmas; seed in most species (except the West Indian) globose or nearly so, with a relatively large, flat and irregular hilum and a minute, appressed-recurved caruncle.

TYPE-SPECIES, *Mozinna spathulata* Ortega.

This is primarily a Mexican group, whose distinctness has been recognized by all students of the Euphorbiaceae. Phylogenetically it appears to be old, most of the species exhibiting dioecism, reduction of vegetative tissue and number of carpels, and adaptation to arid conditions. Its nomenclatural history has been somewhat involved, several names having been applied to it and to its subdivisions. The name *Curcas*, first used by Grisebach for the name of a section, is untenable in the sectional category because of the sectional names *Mozinna* and *Eucurcas* previously proposed by Baillon. The latter was used by Mueller for a subsection, but cannot be used for a section of *Jatropha* because of the existence of sect. *Eucurcas* Pax. The section *Mozinna*, as I interpret it, is essentially identical in circumscription with sect. *Curcas* as used by Mueller, and with subgenus *Curcas* of Pax. The group was divided by Mueller into three subsections based chiefly upon the method



of branching of the inflorescence; in this course he was followed closely by Pax; in general I agree with their system except that I should not separate the group of species with reduced inflorescences (referred by them to *Mozinna*) from obviously closely related species on the basis of this single character. I should separate the following subsections:

1. Plants probably chiefly monoecious, or if dioecious the pistillate flowers in stout, long-stalked inflorescences; lowest branch of the inflorescence regularly alternate, with no flower in the axil; corolla yellow to green; seed more or less elongated or flattened, chestnut-brown to black; fruit often (always ?) fleshy, often semi-drupaceous ..... Subsect. *Eucurcas* Muell. Arg.

1. Plants chiefly dioecious or, if monoecious, the pistillate flowers few in the lowest forks of the cymes; pistillate inflorescences reduced, few-flowered, sessile or essentially so; branches of the staminate inflorescence all opposite or subopposite, with a terminal flower in the fork; corolla white to pink or red, (rarely yellow ?); seed usually globular, varying from gray to dull brown; fruit definitely capsular, not fleshy ..... Subsect. *Mozinna* (Ortega) Muell. Arg.

#### 4a. Subsect. *EUCURCAS* Muell. Arg. in DC. Prodr. 15(2) : 1080. 1866.

*Jatropha*, sect. *Curcas*, subsect. *Eucurcas* Muell. Arg., i.e.; *Curcas* Adans. Fam. Pl. 2: 356, as to type. 1763; *Castiglionia* R. & P. Fl. Per. 139, as to type. 1794; *Curcas*, sect. *Eucurcas* Baill. Etud. Gen. Euphorb. 314. 1858; *Jatropha*, sect. *Curcas* Griseb. Fl. Br. W. Ind. 36, as to type, 1864; *Jatropha*, subgenus *Curcas* Adans. ex Pax, Natürl. Pflanzenfam. 3(5) : 74, as to type. 1890; *Jatropha*, subgen. *Curcas*, sect. *Eucurcas* Pax, i.e.; *Jatropha*, subgen. *Curcas*, sect. *Castiglionia* (R. & P.) Pax, Pflanzenreich IV. 147: 76. 1910.

#### TYPE-SPECIES, *Jatropha Curcas* L.

The species in this subsection, other than *J. Curcas*, are so poorly known that they are associated in this manner as a tentative arrangement only. *Jatropha Andrieuxii* and *J. Pseudo-Curcas* have apparently been collected not more than twice or thrice each. Provisionally the three species may be separated as follows:

1. Seeds black, encrusted-striate, 15–22 mm. long; plants glabrous or with more or less flocculent tomentum; inflorescence expanded, loosely flowered, with small bracts; widely cultivated ..... *J. Curcas*.

1. Seeds chestnut-brown to almost black, more or less lustrous, smooth, 10–15 mm. long; plants uniformly and thinly strigulose to pilose or tomentose; inflorescence various ..... 2.

2. Inflorescence expanded, loosely flowered, with small bracts; leaves uniformly and thinly strigulose on both surfaces with sharp whitish hairs; seeds chestnut-brown, 13–15 mm. long, 11–12 mm. wide .. *J. Pseudo-Curcas*.

2. Inflorescence subcapitate, the bracts and sepals foliaceous, the former up to 4 cm. long; leaves densely pilose above, more or less tomentose beneath; seed lustrous, almost black, 10–12 mm. long, 7–8 mm. wide . *J. Andrieuxii*.

#### 1. *JATROPHA CURCAS* L. Sp. Pl. 1006. 1753.

The original range of *J. Curcas* doubtless included the *tierra caliente* of southern Mexico and Central America, but as it is widely planted and has been so since before the advent of Europeans in the New World, it is not

now possible to say more than this. There are records of its occurrence in the West Indies early in the 16th century, and it may be native there. Morphologically it varies but little; specimens from all parts of its range, in both Hemispheres, are quite uniform in characters. In western Mexico, however, the prevailing form of the species is one differing from the usual type by the development of a considerable amount of flocculent reddish tomentum, especially in the inflorescence; this form appears unquestionably to be indigenous in the region from Colima to central Sinaloa, and occasional individuals from the area between Guerrero and Guatemala approach it in degree of pubescence and may likewise represent a part of the native population of this species. The usual form found in cultivation and as a roadside or dooryard tree is almost glabrous or has a relatively small amount of (usually yellowish) tomentum in the inflorescence.

1a. *JATROPHA CURCAS* var. *rufus* McVaugh, var. nov. A planta typica foliis junioribus ramis inflorescentiae dense pubescentibus, bracteis calycibusque flocculose rufo-tomentosis, differt. Flores seminaeque ut in forma typica.

TYPE collected at Ymala [Imala], Sinaloa, Aug. 16 to 25, 1891, by Edward Palmer (no. 1413); specimen in the United States National Herbarium. Additional specimens examined: SINALOA: Without locality, *J. G. Ortega* 7065 in 1933 (F), 7299 in 1934 (F); Mazatlán to Villa Unión, *L. H. McDaniels* 14, Aug. 6, 1935 (F); COLIMA: Colima, *Edw. Palmer* 23, July 1897 (US).

2. *JATROPHA PSEUDO-CURCAS* Muell. Arg. *Linnaea* **34**: 208. 1865.

This species is known but from the type collection, made by Liebmann in Oaxaca, from Barranca de Panoaya, Veracruz (*Purpus* 8816, CAL), and from a collection (*G. B. Hinton* 4300) made between Salitre and Cañitas, Temascaltepec, E. de México, July 10, 1933. It much resembles *J. Curcas* but may be distinguished from that species by the thin reddish-yellow tomentum of the inflorescence, by the pubescence of the leaves and by the seeds. The fruit is unknown to me. Hinton notes that the flowers are white, and that the vernacular name is "Piñoncillo." Mueller states that the style-column is longer than the stigmas, in contrast to *J. Curcas* in which he states the reverse to be true; I have not been able to confirm this difference, finding the column short in both species, although with some individual variation.

3. *JATROPHA ANDRIEUXII* Muell. Arg. *Linnaea* **34**: 208. 1865.

This plant is of rather doubtful affinity, having been placed by Mueller in *Adenorhopium* because of the supposedly distinct petals, but evidently akin to *J. Curcas* and other species of the section *Mozinna* in the large dark seeds with small caruncle, the very large foliaceous calyx-lobes of the pistillate flowers, the small stipules, the leaves similar to those of *J. Curcas* and *J. Pseudo-Curcas*, the 10 stamens, and the plant-habit; the corolla-lobes,

instead of being free as stated by Mueller, are (at least in the pistillate flower) connate up to half their length. The species differs from all other species known to me, however, in the long-stalked, sub-capitate (pistillate) inflorescence with leafy bracts surpassing and concealing flowers and fruits; the styles, moreover, are bifurcate but slender, apparently lacking the fleshy stigmatic lobes characteristic of *Mozinna*, and the corolla (pistillate) is entirely glabrous. I have seen no staminate flowers, but Mueller's description supplies most of the characters usually found in the section; he says that the teeth of the staminate calyx are entire, 3-4 mm. long (i.e. much smaller than the pistillate), the petals villous within, the filaments 10.

The species is known but from the original collection, made by Andrieux (no. 114) between Chila, Puebla, and Huahuapan, Oaxaca, and from a collection made by Pringle near Iguala, Guerrero, Oct. 24, 1900. The foliage resembles that of *J. Curcas*, but the leaves are uniformly and densely soft-pilose on both surfaces, and the petioles are relatively short and stout (2 mm. in diameter, mostly 2-5 cm. long) and tomentose. The bracts of the inflorescence are undulate and often lobulate, up to 2 cm. wide and 3-4 cm. long; the sepals (pistillate) are often half as large. The capsule is ovoid, pointed, 13-15 mm. long and wide, apparently somewhat fleshy and tardily dehiscent; the seed is lustrous, almost black, 10-12 mm. long, 7-8 mm. wide, 5-6 mm. thick.

4b. Subsect. MOZINNA (Ortega) Muell. Arg. in DC. Prodr. 15(2) : 1081. 1866.

*Jatropha*, sect. *Curcas*, subsect. *Mozinna* Muell. Arg., i.e., as to type; *Mozinna* Ortega, Dec. Pl. 8: 104, as to type. 27 Ja., 1799; *Lourcira* Cav. Ic. 5: 17. [late] 1799; *Curcas*, sect. *Mozinna* (Ortega) Baill. Etud. Gen. Euphorb. 315. 1858; *Jatropha*, sect. *Curcas*, subsect. *Lourcira* (Cav.) Muell. Arg., op. cit. 1076; *Zimapania* Engl. & Pax, Natürl. Pflanzenfam. 3(5) : 119, 1891; *Jatropha*, subgenus, *Curcas*, sect. *Lourcira* (Cav.) Muell. Arg. ex Pax, Pflanzenreich IV. 147: 74. 1910; sect. *Mozinna*, subsect. *Brachyblastae* Pax, op. cit. 81, in clavi; subsect. *Canescentes* Pax, l.c.

TYPE-SPECIES, *Mozinna spathulata* Ortega.

There are about 20 known species of this subsection; most of them are well marked and easily recognized, but not more than half of them are well known, the others having been collected not more than a few times each. The characters used by Mueller and Pax to divide the group seem to produce an unnatural arrangement, and I am at a loss to effect any division within the subsection unless *J. Gaumcri*, an endemic of the Yucatan peninsula, be removed entirely from the section *Mozinna* on the bases of its uniquely divided styles. *J. fremontoides*, known only from the original collection in southern Oaxaca, is likewise unique in its congested and capitate inflorescence with imbricate paleaceous bracts, and its large fimbriate caruncle suggests no relationship to *Mozinna*, but its flowers are those of that section and apparently it must be placed therein unless a new group be established for it. The dioecious members of the subsection have for the most part seeds

which are characterized by their nearly globular shape and their very small caruncles, while the monoecious members, including *J. Gaumeri*, *J. fremontioides* and the two West Indian species, *J. divaricata* and *J. hernandiaefolia* have seeds more nearly like those of *Adenorhopium*. Seeds of several species are unknown to me, however, and it seems unwise to make any further attempt at classification based upon this single character.

The remaining members of the subsection agree to a remarkable degree in reproductive characters, especially when one considers the rather excessive variation which they exhibit in vegetative structure, and on this account it seems unnecessary to designate any formal series or other categories, although two such series are superficially apparent. The first of these includes *J. cuneata*, *J. dioica*, *J. neopauciflora*, and perhaps others, and is characterized by the narrow, cuneate, and almost sessile leaves of the included species; the other series includes species with broader, ovate or cordate leaves with slender petioles. The gap between the series is bridged by such species as *J. sympetala*, *J. Standleyi*, *J. Ortegae*, and *J. Riojac*, as far as leaf-characters are involved. The members of the first series often have the inflorescences so reduced as to appear fasciculate, but varying degrees of reduction are found in individual plants, and similar conditions may be found in *J. cinerea* and other species, so that a more or less continuous intergrading series can be established from species with few-flowered and much reduced cymes to those with much branched many-flowered types. Any attempt to subdivide the subsection along these lines would seem to be a purely arbitrary one.

The following purely artificial key will serve to distinguish the species:

1. Leaves broadly peltate ..... 2.
2. Plants monoecious; leaves up to about 12 cm. long, ovate, unlobed or 3-lobed, mostly abruptly and sharply acuminate; Puerto Rico and Hispaniola ..... *J. hernandiaefolia*.
2. Plants dioecious; leaves mostly 18-30 cm. long, orbicular-ovate, usually with 3 or 5 rounded lobes; Sinaloa to Michoacán ..... *J. platyphylla*.
1. Leaves not peltate (or in exceptional individuals the basal margins of the blade produced into a narrow wing 1-2 mm. wide) ..... 3.
3. Inflorescence capituliform, monoecious, the staminate flowers sessile and the bracts closely imbricate; Oaxaca ..... *J. fremontioides*.
3. Inflorescences not capituliform, usually dioecious or, if monoecious, the staminate flowers pedicellate in slender cymes ..... 4.
4. Plants monoecious, glabrous, with entire, ovate, acuminate leaves ..... 5.
5. Style-branches flattened, incised-toothed, stamens 8; Yucatan Peninsula ..... *J. Gaumeri*.
5. Style-branches slender, with thickened fleshy stigmas; stamens (18-)10; Jamaica ..... *J. divaricata*.
4. Plants mostly dioecious, variously pubescent or glandular; style-branches filiform with capitate or somewhat elongate fleshy stigmas; leaves various; southern and western Mexico ..... 6.

6. Leaves cuncate, relatively narrow (those on shoots sometimes pinnately lobed); petioles normally short (5-10 mm. long or less, or sometimes longer on vigorous shoots), the leaves mostly appearing sessile or nearly so ..... 7.
7. Leaves green and glabrous or nearly so above, persistently and prominently whitened and waxy-papillose beneath ..... *J. sympetala*.
7. Leaves either glabrous or pilose, never whitened and papillose ..... 8.
8. Stipules 5-8 mm. long, covered at least at base with bright ferrugineous hairs; leaves pilose and somewhat whitened on both surfaces; staminate corolla 6-9 (12) mm. long; anthers 1.3-1.7 mm. long ..... *J. neopauciflora*.
8. Stipules 1-1.5 mm. long or less (rarely 3.5 mm.), canescent at base with pale hairs; leaves essentially glabrous on both surfaces at maturity; staminate corolla 4-7 mm. long; anthers 1 mm. long or less ..... 9.
9. Leaf-blades entire, 2-3 times as long as wide, with one pair of lateral veins in addition to the basal pair; staminate cymes evidently branched, slender, 0.7-1.5 cm. long; bracts and sepals ciliate on tips and margins; intricately branched shrubs of the Sonoran Desert, with hard woody twigs ..... *J. cuneata*.
9. Leaf-blades often 3-lobed on vigorous shoots, mostly much more than 3 times as long as wide, with two pairs of lateral veins in addition to the basal pair; staminate cymes greatly reduced, the flowers apparently in dense terminal or axillary clusters; bracts and sepals rather uniformly pubescent, often canescent; sparingly branched shrubs, Texas and eastern Mexico, with parenchymatous twigs that shrink conspicuously upon drying ..... 10.
10. Leaf-blades 2.5-6 times as long as wide, mostly 6-10 mm. wide ..... *J. dioica* var. *sessiliflora*.
10. Leaf-blades 6-17 times as long as wide, mostly 1-4 mm. wide ..... *J. dioica* var. *graminea*.
6. Leaves relatively broad, often more or less cordate, varying to oblong or oval or, if narrow, then with conspicuous slender petioles ..... 11.
11. Mature blades up to 10-12 cm. long and wide, densely rufous-tomentose beneath over the entire surface ..... 12.
12. Blades cordate, broadly ovate, entire or with blunt shallow lobes; Puebla and Oaxaca ..... *J. rufescens*.
12. (Mature blades unknown, but probably densely pilose or tomentose, with 3-5 ovate, long acuminate lobes; Sonora. *J. malacophylla*).
11. Blades mostly smaller, either glabrous, glandular or vari-ously pubescent, but the mature blades not rufous-tomentose (sometimes cinereous-tomentose in *J. cinerea*) ..... 13.
13. Blades not lobed, ovate, oval or oblong, cuneate to rounded at base, not cordate, pinnately veined (the lowest pair of veins often larger than the others) ..... 14.
14. (Petioles puberulent; blades usually cinereous-tomentellous and rounded or truncate at base, suggesting the cordate condition; Sinaloa, Sonora, Baja California ..... exceptional forms of *J. cinerea*).

14. Petioles glabrous; blades cuneate or rounded at base, glabrous or nearly so ..... 15.
15. Blades with several cupuliform glands on the margins near base ..... 16.
16. Petioles very slender; lower surface of blades very minutely puberulent; Sinaloa ..... *J. Ortegae*.
16. Petioles stout (to 2 mm. in diameter); blades glabrous; Oaxaca ..... *J. Standleyi*.
15. Blades entire, glabrous; Puebla (see also forms of *J. sympetala*, which may have the blades almost without the normal covering of white papillae) ..... *J. Riojae*.
13. Blades often lobed, usually definitely cordate at base, ovate to reniform, palmately veined at base (at least in leaves with lobes) ..... 17.
17. Blades with 3-5 sharp lobes, these ovate-deltoid with acuminate tips ..... 18.
18. Blades not glandular, densely velutinous-pilose (mature blades unknown); Sonora and Sinaloa ..... *J. malacophylla*.
18. Blades more or less beset with cupuliform ("pinhead") glands at least on the basal lobes; pubescence of blades more or less confined to the veins and margins; southern Mexico ..... 19.
19. Leaves more or less glaucous, with soft, usually bright red, hairs; inflorescence glabrous except the bracts, which are red-hirsute within; México to Oaxaca ..... *J. ciliata*.
19. Leaves not glaucous, stiff-puberulent, the hairs usually whitish; inflorescence canescent; Oaxaca ..... *J. Alamani*.
17. Blades entire to shallowly lobed or toothed ..... 20.
20. Blades irregularly crenulate, the crenulations at least when young with sessile glands ..... 21.
21. Plants entirely glabrous; blades mostly 3 cm. long and wide, or less, often wider than long, abruptly and prominently blunt-acuminate; Arizona and Sonora ..... *J. cardiophylla*.
21. Inflorescence cinereous-tomentellous, glabrescent; plants otherwise glabrous; blades often 5-8 cm. long, ovate, longer than wide, acute or short-acuminate; southern Baja California ..... *J. vernicosa*.
20. Blades entire to toothed or lobed; foliar glands, if present, stalked ..... 22.
22. Leaves, inflorescences and twigs more or less cinereous-tomentellous; blades usually not glandular or lobed but rarely one or both; north-western Mexico ..... *J. cinerea*.
22. Plants not cinereous-tomentellous; blades usually with stalked glands ..... 23.
23. Blades unlobed, ovate, 3-6 cm. wide, green, the margins rather densely beset with stalked glands; bracts of the staminate inflorescence ciliate and hispidulous on backs; Jalisco to Sonora ..... *J. cordata*.

23. Blades often somewhat lobed, at maturity 10–15 cm. wide, usually glaucous, sparingly glandular; bracts red-hirsute within; México to Oaxaca ..... *J. ciliata*.

*Jatropha Alamani* Muell. Arg. is known only from the vicinity of Tehuantepec, Oaxaca, where collected by Alaman in 1832 (TYPE in herb. DC., Field Mus. neg. 7161!) and by Orcutt (no. 5329!) in 1910. I have not seen pistillate material, and the fruits and seeds are unknown.

*J. canescens* (Benth.) Muell. Arg. is to be relegated to the synonymy of *J. cinerea* (Ortega) Muell. Arg., a characteristic shrub of the areas adjacent to the Gulf of California. *Jatropha cinerea* consists of several races distinguished by leaf-shape and quality of pubescence; the principal ones are as follows:

1. A race localized near the tip of the peninsula of Baja California. The leaf-blades are large for the species, 5–8 (10) cm. wide and long, mostly cordate with rounded basal lobes, the midrib 4–6 (7) cm. long, the basal pair of veins often spreading at an angle of 180° or somewhat reflexed. The blade is usually pointed, its tip acute to acuminate or rounded, the lower surface thinly tomentose and whitened, the upper surface and the petiole sparsely puberulent. The branches appear to be stouter than in other races. I have seen 10 collections of this race, which is known as “lumboi” (Bailey) or “lomboy” (Collins et al.). A collection from Guamuchil, Sinaloa, *Shreve 6391*, is similar to Baja California material.

2. A rather restricted race found, in its most typical form, along the northern coast of Sonora about Kino Bay, and on the gulf coast of Baja California south about to latitude 26°. The leaf-blades are (2)2.5–4 (or 6) cm. wide and long, mostly rounded or reniform, often folded on herbarium sheets, rounded or truncate or obscurely cordate at base, the basal lobes, if any, rarely extending below the base of the veins, the midrib thus the longest part of the blade; basal pair of veins often undeveloped, (veins then one pair only in addition to the midrib), but if present usually evidently ascending. Blade usually rounded at tip but sometimes obtusely pointed; pubescence sparse, and sometimes entirely wanting from mature leaves. I should refer to this race 7 collections from Sonora, one from Sinaloa (San Blas, *M. E. Jones 23327* in the Field Museum) and one from Baja California (Loreto, *Jones 27547*).

3. Apparently the most common race, from northern Sonora (or southern Arizona) to central Sinaloa. I have seen 15 collections of this, distinguished from no. 2 by the rather dense and generally distributed pubescence, which makes the young growth and the inflorescence felty-white; the leaves are essentially like those of no. 2, but are usually permanently and densely tomentose beneath and on the petioles, but sparsely pubescent above. The blades are sometimes sparsely glandular-toothed or divided into three broad rounded or truncate lobes, especially on vigorous shoots. A collection from “Quitobaquita,” made by Schott in August 1855, now in the Field Museum, may have been taken in what is now Arizona, and if so represents the first definite record of this species from the United States.

4. A specimen collected at Magdalena Island, Baja California, by T. S. Brandegee, Jan. 12, 1889, has the leaves tomentose on both surfaces; this apparently represents typical *Mozinna canescens* Benth., also first collected on Magdalena Island.

*Jatropha cordata* (Ortega) Muell. Arg. is relatively common from central Sonora to northern Sinaloa and extends sparingly south to Jalisco. In this species pubescence is apparently somewhat correlated with geographic distribution; all material from Sonora and Chihuahua is glabrous or essentially so, but all from Jalisco and most from Sinaloa (except from the extreme north) is rather densely stiff-pubescent. A collection from southern Zacatecas, *Rose 2415*, is glabrous. A fragment in the Field Museum herbarium, probably from the type plant of *Loureira glandulosa* Cav., is the pubescent form, as in no. 4245 of the collection made by Sessé, Mociño and Maldonado; presumably Ortega's original *Mozinna cordata* was of the same type.

*Jatropha dioica* Sessé in Cerv. As pointed out elsewhere (McVaugh, 1945, this name must replace the well known *J. spathulata* (Ortega) Muell. Arg.

The type of *Jatropha malacophylla* Standl. (the only collection so far distributed under this name) is apparently conspecific with all material distributed as *J. platanifolia* Standl. (including the type). The species discussed by Gentry in his *Rio Mayo Plants* (Carneg. Inst. Wash. Publ. 527: 166, etc. 1942) under the name of *J. platanifolia* should therefore be called *J. malacophylla*. The type of *J. malacophylla* differs from that of *J. platanifolia* in having ciliate but otherwise nearly glabrous sepals in the staminate flowers; the sepals of *J. platanifolia* vary from very nearly glabrous to rather densely hirsute. In addition, the leaves of the type of *J. malacophylla* (an immature specimen) are predominantly 3-lobed, with young 5-lobed leaves just beginning to appear, while most leaves of the type and other specimens of *J. platanifolia* (even when immature) are 5-lobed. In view of the exact correspondence in other respects between the two "species," the above differences appear to represent individual variations rather than more fundamental ones.

*J. neopauciflora* Pax is known only from a small area in the vicinity of Tehuacán, in southern Puebla. Here is probably to be referred *J. Harmsiana* Mattf., based on a collection made by J. A. Purpus in April 1922, in "Kalkberge bei Telmacan." This collection was in the Berlin herbarium and presumably, has been destroyed. The type-locality is given as Tehuacán by Pax (Pflanzenreich IV. 147. XVII: 204. 1924).

*J. Ortegae* Standl. is known to me only from the type collection and from another (*J. G. Ortega 7413*) from the same region, southern Sinaloa. It is evidently very closely related to *J. cordata*, and also to *J. Riojae* Miranda, of Puebla.



*J. Standleyi* Steyermark appears to be a very much localized species of southern Oaxaca. It is known only from the type, collected by Matuda at Tehuantepec in 1936, and from a living tree in the collection of the Missouri Botanical Garden, thought to have come from material collected by C. R. Orcutt at Tehuantepec in 1910. A specimen in the Field Museum, collected in "Mexico" in 1791 by Haenke, appears to be of this species. The type of *J. Standleyi* is in the herbarium of the University of Michigan, as noted by Lundell (1941), not at the Field Museum as stated in the original description.

The type of *Jatropha sympetala* Standl. & Blake (from Playa de Coyula, Oaxaca, *Reko* 350!) has entire oval leaf-blades up to 5 cm. wide and 8 cm. long, on slender petioles up to 1.5 cm. long; the lower surface is pale and densely papillose, but not strongly whitened. It suggests on the one hand a relationship with *J. Riojae* Miranda, which has similarly shaped but smaller and greener leaves, and on the other a relationship with *J. Ortegae* Standl., which has pubescent blades of similar shape but with glandular margins. I should refer no other specimens to *J. sympetala* except the following, in both of which the lower surfaces of the leaves are much more conspicuously whitened than in the type: Tehuantepec, Oaxaca, *Orcutt* 5259; Mazatlán, Sinaloa, *Rose* 1388. The Orcutt specimen differs from the others in having glandular margins on some of the leaves, and both Orcutt's and Rose's specimens differ from the type in the more elongate and cuneate short-petiolate leaves, which in shape suggest those of *J. dioica*.

*Jatropha vernicosa* Brandg. appears to be a distinct species endemic in the relatively mesophytic habitat of canyons of the higher mountains of southern Baja California. Standley (1923) says "Rather doubtfully distinct from *J. cordata*," but the affinities of *J. vernicosa* seem to be as much with *J. cardiophylla* as with *J. cordata*. It is easily distinguished from the latter by its lack of stipitate glands. The following specimens are referred here: Corral Piedra, *T. S. Brandegees*, Sept. 9, 1893 (Type, CAL; GH); Sierra de San Francisquito, *Brandegee* 545, Oct. 20, 1890 (CAL); Arroyo Hondo, Sierra Giganta, *Gentry* 4150 (Mo).

#### DOUBTFUL ENTITIES

Sect. *Stigmatosae* Pax & Hoffm. Pflanzenreich IV. 147. XVII: 192. 1924. This was assigned to subgenus *Adenoropium*, apparently on the basis of habital resemblance to species of sect. *Tuberosae*. The description of *J. stigmatosa*, the only species of the section, suggests a *Ditaxis* but I have not seen the type. The section was based principally upon the character of the filiform, radiating styles.

*Jatropha catingae* Ule and *J. palmatifolia* Ule I cannot place from the descriptions. Both are said to have 6 stamens and the leaf-margins entire and eglandular, and there is nothing else like this known in the genus.

## INDEX TO THE AMERICAN SPECIES

[*Polymorphae*, I; *Macranthae*, II; *Adenorhopium*, III; *Mozinna*, IV. Names considered to represent synonyms are italicized and followed by what is most probably the correct specific name, inclosed in brackets. A brief basis for the assignment of each species to a section or to synonymy is given in parentheses. In addition to the specimens cited below, I have examined all the material of *Jatropha* in the following herbaria: United States National Herbarium, Herbarium of the National Arboretum and the herbarium of the Missouri Botanical Garden. Certain material, chiefly Mexican, has been examined from the following sources: Arnold Arboretum, Gray Herbarium, Chicago Museum of Natural History (cited herein, as always previously, as the Field Museum), New York Botanical Garden, University of Michigan, University of California at Berkeley. To those in charge of these herbaria I am grateful for many kindnesses. Mr. Paul C. Standley is especially to be thanked for his efforts in assembling for me all the specimens of *Jatropha* from the herbarium of Sessé and Mociño.]

- acerifolia* Salisb. [Curcas] (fide Ind. Kew.)  
*acuminata* Desr. [integerrima] (Description)  
 Alamani Muell. Arg., IV (FM neg. 7161!)<sup>3</sup>  
 Andrieuxii Muell. Arg., IV (FM neg. 32488!)  
 angustifolia Griseb., I (Description)  
*antisiphilitica* Speg. [†Isabelli] (Pax, 1910; Lourteig & O'Donell, 1943)  
*arizonica* I.M. Johnst. [macrorhiza var. septemfida] (Type, GH!)  
 Augusti Pax & Hoffm., II (?Phototype, FM neg. 5379!)  
*Berlandieri* Torr. [cathartica] (Type, NY!)  
 Berterii Spreng. [unknown]  
 Bornmülleri Pax, III (Description)  
 brachypoda Pax, III (Description)  
 breviloba (Morong) Pax & Hoffm., III (Isotype, US!)  
*canescens* (Benth.) Muell. Arg. [cinerea] (Voy. Sulph. pl. 25)  
 cardiophylla (Torr.) Muell. Arg., IV (type, NY!)  
 cathartica Ter. & Berl., II (Description)  
 catingae Ule [doubtful; see above]  
*ccreidiphylla* Standl. [not *Jatropha*] (Contr. U. S. Nat. Herb. 23: 1669)  
*ciliata* Sessé, IV (Type, Madrid!)<sup>4</sup>  
*ciliata* Muell. Arg., II (FM neg. 24382!)<sup>5</sup>

<sup>3</sup> The "phototypes" from the series assembled by the Field Museum are designated by negative number as in this case; in this table I have not distinguished between photographs of actual types and those of isotypes (for example, neg. 24388, *J. macrorhiza*); when the photograph is not certainly of type material, I have indicated this by a question-mark preceding the word "phototype."

<sup>4</sup> The types of species of *Jatropha* described by Sessé or in the posthumous works of Sessé and Mociño must of necessity be arbitrarily chosen—lectotypes. Often there are in the herbarium of Sessé, Mociño and Maldonado several mounted sheets of the same species, bearing the same name and number. In such cases I have selected as type, whenever possible, the best sheet from among those not accessioned by the Field Museum; these are cited in this table as having been seen in the Madrid herbarium, although all are now on deposit in Chicago. In some cases (e.g. *Jatropha dioica* and *J. edulis*) I have seen only the sheets of these species accessioned by the Field Museum; these are mentioned in the table with the designation "type-collection."

<sup>5</sup> The specimen photographed under this number is from the Delessert Herbarium, collected by Pavon (no. 108), supposedly in Mexico. It was determined by Mueller as *J. ciliata*, and is without doubt the Peruvian plant currently passing as *J. ciliata* Muell. Arg. The type of this species, however, was collected "in Peruvia prope Huanaca," and

- cinerea (Ortega) Muell. Arg., IV (Description)
- clavuligera Muell. Arg., III (FM neg. 7160!)
- coccinea Hort. ex Steud. [?integerrima]
- coccinea Hort. ex Link [integerrima] (Pax, 1910)
- cordata (Ortega) Muell. Arg., IV (Description)
- cuneata Wiggins & Rollins, IV (Isotype, AA!)
- cuneifolia Sessé & Moc. [unknown; said to be from Puerto Rico]
- Curcas L., IV (Description)
- decipiens M. E. Jones [not Jatropha] (C. V. Morton in Contr. U. S. Nat. Herb. 23(2), in press)
- dioica Sessé, IV (Type collection, F!)
- dissecta (Chod. & Hassl.) Pax, III (Description)
- divaricata Sw., IV (Description)
- divergens (Pohl) Baill. [mollissima] (fide Muell. Arg., 1866)
- diversifolia A. Rich. [integerrima] (Description)
- edulis Sessé [Curcas] (Type-collection, F!)
- eglandulosa Pax, III (FM neg. 5384!)
- elegans (Pohl) Klotzsch [gossypifolia] (Description)
- elliptica (Pohl) Muell. Arg., III (Pohl, Pl. Bras. 1c. 1: pl. 9)
- excisa Griseb., III (FM neg. 5385!)
- flabellifolia Pax & Hoffm. [Paxii] (Jour. Arn. Arb. 24: 168)
- flavovirens Pax & Hoffm., III (FM neg. 5386!)
- fremontioides Standl., IV (Type, F!)
- Gaumeri Greenm., IV (Type, F!)
- glauca Griseb. [angustifolia] (Muell. Arg., 1866, p. 1093)
- glaucovirens Pax & Hoffm. [integerrima] (Isotype, Mo!)
- gossypifolia L., III (Description)
- grandifrons I. M. Johnst. [ciliata Sessé] (Type, GH!)
- grossidentata Pax & Hoffm., II (?Phototype, FM neg. 5387!)
- guaranitica Speg., III (Description)
- Harmsiana Mattf. [neopauciflora] (Description)
- hastata Jacq. [integerrima] (Jacq. Sel. Stirp. Am. 256, pl. 183, f. 47, pl. 173, f. 54)
- hernandiaefolia Vent., IV (Description)
- heterophylla Sessé & Moc. [hernandiaefolia] (Type, Madrid!)
- Hieronymi Kuntze, II (?Phototype, FM neg. 5390!)
- hippocastanifolia Croiz., III (Description)
- Hoffmanniae Croiz., II (Description)
- Humboldtiana McVaugh, II (Description)
- induta (Chod. & Hassl.) Pax, III (FM neg. 24384!)
- integerrima Jacq., I (Description)
- intercedens Pax, III (FM neg. 5393!)
- intermedia (Chod. & Hassl.) Pax, III (Description)
- Isabelli Muell. Arg., III (FM neg. 24385!)
- Jacquini (Pohl) Baill. [gossypifolia] (Mueller, 1866; Pax, 1910)
- Katharinæ Pax, III (Pax, 1910, fig. 8)
- Lacerti Silva Manso [elliptica] (fide Pax, 1910, p. 62)
- Loeflingii Aresch. [unknown]
- longipedunculata Pax & Hoffm. [Hoffmanniae] (Jour. Arn. Arb. 24: 168)
- luxurians (Pohl) Baill. [mollissima] (Muell. Arg., 1866, p. 1091)
- macrantha Muell. Arg., II (FM neg. 8496!)
- macrocarpa Griseb., II (FM neg. 5394!)
- macrorhiza Benth., III (FM neg. 24388!)
- var. septemfida Engelm., III (Isotype, US!)
- malacophylla Standl., IV (Type, US!)
- Malmeana Pax & Hoffm., III (Description)
- Martiusii (Pohl) Baill., II (Description)
- minor Urb., I (Description)
- mitis Sessé & Moc. [unknown]
- mollissima (Pohl) Baill., II (Description)
- molucensis Sessé & Moc. [integerrima] (type, Madrid!)
- multifida L., II (Description)
- multiflora Pax & Hoffm. [macrocarpa] (Lourteig & O'Donell, 1943)
- mutabilis (Pohl) Baill., II (Description)
- neopauciflora Pax, IV (Contr. U. S. Nat. Herb. 12: pl. 22)
- nudicaulis Benth., II (Description)
- officinalis "Mart." [elliptica] (Pax, 1910)
- olivacea Muell. Arg. [ciliata Sessé] (Description)
- opifera Mart. [elliptica] (fide Pax, 1910)
- Ortega Standl., IV (Type, F!)
- pachypoda Pax, II (FM neg. 5396!)
- palmatifolia Ule [doubtful; see above] (FM neg. 5397!)

was cited by Mueller as follows: "(Dombey ! Ruiz ! in hb. Mus. paris. et berol.)" (Linnaea 34: 210), so that the Pavon specimen, while conceivably part of the type-collection, certainly is not the type.

*palustris* Sessé & Moc. [unknown]  
*panduraefolia* Andr. [integerrima] (Andr.

Bot. Repos. 4: pl. 267)

*papyrifera* Pax & Hoffm., II (Description)  
*pauciflora* Griseb. [integerrima] (Isotype, US!)

*pauciflora* (Rose) Pax [neopauciflora] (Type, US!)

*Paxii* Croiz., I (Pax, 1910, fig. 20)

*pedatipartita* Kuntze, III (Isotype, US!)

*Peiranoi* Lourt. & O'Don., III (Lilloa 9: 135, fig. 17, pl. 14)

*peltata* Sessé [unknown] (Bull. Torrey Club 72: 34. 1945)

*peltata* HBK. [Humboldtiana] (Bull. Torrey Club 72: 35. 1945)

*platanifolia* Standl. [malacophylla] (Type F!)

*platyphylla* Muell. Arg., IV (FM neg. 34049!)

*podagrica* Hook., II (Bot. Mag. pl. 4376)

*Pohlana* Muell. Arg. [mollissima] (See above)

*portoricensis* Millsp. [hernandiaefolia] (Description)

*Pseudo-Cureas* Muell. Arg., IV (FM neg. 21554!)

*puncticulata* Pax & Hoffm., III (Description)

*purpurea* Rose, III (Type, US!)

*purpurea* Rose & Pax ex Pax [purpurea

Rose, which is based on same type]

*ribifolia* (Pohl) Baill., III (Description)

*ricinifolia* Pax, II (Pax, 1910, fig. 11)

*rigidifolia* Pax & Hoffm., III (Description)

*Riojae* Miranda, IV (Isotype, F!)

*Robertii* S. Moore, II (Description)

*rufescens* Brandg., IV (Isotype, GH! F!)

*spathulata* (Ortega) Muell. Arg. [dioica]

(Orteg. Pl. Dec. pl. 13)

*Standleyi* Steyerf., IV (Type, MICH!)

*staphysagrifolia* Mill. [gossypifolia] (Description)

*stigmatisa* Pax & Hoffm. [unknown; see note above]

*sympetala* Standl. & Blake, IV (Type, US!)

*tacumbensis* Pax & Hoffm., III (Description)

*thyrsantha* Pax & Hoffm., III (FM neg. 5403!)

*transiens* Pax, III (FM neg. 24390!)

*tupifolia* Griseb., I (Description)

*vernica* Brandg., IV (Type, CAL!)

*villosa* (Pohl) Baill. [mollissima] (Muell. Arg., 1866)

*Weberbaueri* Pax & Hoffm., II (Pax, 1910, fig. 16)

*Weddelliana* Baill., II (Description)

*yucatanensis* Briq. [Cureas] (FM neg. 24393!)

## DIVISION OF PLANT EXPLORATION AND INTRODUCTION

### BUREAU OF PLANT INDUSTRY STATION, BELTSVILLE, MARYLAND

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## A REPORT OF SOME RECENT COLLECTIONS OF RUBIACEAE FROM ECUADOR

WILLIAM CAMPBELL STEERE

One of the outstanding publications concerned with the botany of the republic of Ecuador has been Paul C. Standley's "The Rubiaceae of Ecuador" (1931), into which he incorporated all available data on this family, and reviewed the classic collections of Richard Spruce and William Jameson. Since 1931 relatively little has been added to our knowledge of the Rubiaceae of Ecuador, although Diels (1937) was able to augment the list with several species, and Acosta-Solís (1943) has recently added a few more.

During 1943 and 1944 large collections of Rubiaceae have been made throughout Ecuador by several botanists engaged in a search for *Cinchona* in behalf of the Office of Foreign Economic Administration (formerly Board of Economic Warfare), a procurement agency of the United States Government. As Senior Botanist and Assistant Director of the Cinchona Mission in Ecuador from July 1943 to September 1944, I had an unexcelled opportunity to collect and study *Cinchona* allies as an integral part of my work.

My chief collecting activity was in the northernmost provinces, Carchi, Imbabura, and Napo-Pastaza, which were well explored; but smaller collections were made in the provinces of Pichincha and León. Moreover, a large collection was made jointly with Dr. W. H. Camp in the valley of the Río Pastaza between altitudes of 3000 and 7500 feet. Although I made several visits to the classical *Cinchona* localities of Loja and Azuay, these visits were unfortunately rapid inspection trips on which there was no time for collecting. The policy of collecting all Rubiaceae has been followed by all the botanists who came later to Ecuador to work for the Cinchona Mission, in order not to overlook any possible sources of quinine, and important collections have already been made by Dr. W. H. Camp, Dr. Ira L. Wiggins, Dr. William B. Drew, Dr. Gerald W. Prescott, and Dr. F. Marion Ownbey.

In such work as that of the Cinchona Mission it was impossible to give attention to the whole of an unfamiliar flora and vegetation. In a futile attempt to understand the ecological relations of a single genus the botanist might attempt to encompass the whole flora, and be baffled by its complexity, finally failing to accomplish or neglecting his basic objective. It was more practicable and much easier to cultivate an alertness in detecting only members of the family to which *Cinchona* belongs. This is exactly the procedure which I developed in my explorations for *Cinchona*. By observing, collecting and studying all Rubiaceae seen in the forests through which I passed,

the possibility of overlooking an unfamiliar or anomalous species of *Cinchona* was automatically avoided.

The practical value of this specialization was demonstrated many times by the discovery of species of *Cinchona* in areas reputedly barren of it. For example, the region of the valley of the Río Pastaza at its junction with the Río Topo has produced many tons of high grade bark during 1943 and 1944, from a form of *Cinchona officinalis* unknown there before our explorations. Richard Spruce spent considerable time in exactly this zone, and the point called "Casha-urcu," which was mentioned in his *Travels* (2: 147), has been one of our highest-yielding areas. Also, *Cinchona officinalis* was found to occur throughout Ecuador along the eastern slope of the Andes, even in the northernmost part, instead of being restricted to Loja and Azuay, as believed previously. Furthermore, in Ecuador the members of the Rubiaceae tend to occur in groups, rather than to have a random distribution through the forest, so that when a zone rich in Rubiaceae is discovered, it may at once be suspected to contain *Cinchona*. Consequently, our careful scrutiny of the forest for all members of the Rubiaceae has had the double virtue that no *Cinchona* could be overlooked amid the complex vegetation, and that the discovery of zones rich in Rubiaceae immediately led to a more intensive search for species of *Cinchona*.

As a result of my special attention to the Rubiaceae during my field work in Ecuador between July, 1943, and September, 1944, I was able to collect 345 numbers, which with very few exceptions belong to the Rubiaceae. In order to know while still in the field the Ecuadorean genera and to determine what genera and species of Rubiaceae might characteristically occur in association with the different species of *Cinchona*, specimens were sent by air express from Ecuador to Dr. Paul C. Standley of the Chicago Natural History Museum for identification. The prompt naming of my collections by the outstanding specialist on Rubiaceae (1930, 1931, 1931a, 1931b, 1936), has been of the utmost value. One of the most practical results of his identification for me of several specimens of *Cephaëlis Jamesonii* collected in the *Cinchona pitayensis* zones of the northernmost provinces, Carchi and Imbabura, was that it made possible the discovery of *C. pitayensis* on the west side of the Volcán de Pichincha, in the latitude of Quito, and its first known occurrence south of the equator. The association of *Cinchona pitayensis* with *Cephaëlis Jamesonii*, and the usefulness of the latter as an indicator, has already been reported upon (Steere 1944).

Dr. Standley has identified all my material and at the same time has checked or corrected the identifications which I was able to make through the use of his "Rubiaceae," a copy of which was my constant companion in the field. The statistics of my collection (56 new species out of 345 collection numbers representing about 150 species in all) illustrate graphically the

incredible richness in Rubiaceae of the Ecuadorian flora, and I am convinced from my own observations that intensive work in any other family of plants would have had equally profitable results. A general collector working in a flora as rich as that of the eastern slopes of the Andes in Ecuador is much less apt to get as large a proportion of new and interesting species as the botanist who works more or less exclusively with a single large family or with several smaller, closely-related ones. It is difficult to remain "sensitized" to several groups at the same time. For example, I found that while I was engrossed in a search for *Cinchona* in particular and the Rubiaceae in general, I was almost blind to the presence of other plants in which I have a special interest. Also, of course, a person specializing in one or a few families will have a much better idea of specific and generic concepts and their distinguishing characters. In fact, a general collector who visits the Oriente of Ecuador during the flowering season is apt to be discouraged by the great profusion of species, because he cannot collect them all in the time at his disposal, and is likely to get mainly the most conspicuous and least interesting ones. Spruce (Travels 2: 207-208) estimated in 1858 that by moving a degree of latitude or longitude, he found about half the plants different. On this basis he calculated that there yet remained to be discovered in the great Amazonian forest "from the Cataracts of the Orinoco to the mountains of Matto Grosso," some 50,000 or even 80,000 new species. This estimate is overwhelming, yet Spruce's experience was more extensive than that of any other botanist before or since, and his judgment in systematic matters has proved to be excellent, more conservative than otherwise. Consequently, where the Amazonian forest impinges upon the eastern flank of the Andes, and is subjected to the influence of altitude and the local climates typical of mountainous regions, there should be an enormous diversity within all families, to which Spruce's enthusiastic remarks on the forests of Canelos, at the base of the Andean foothills of Ecuador, will testify. In the course of our two weeks work in the valley of the Río Pastaza between Puyo and Baños, Dr. Camp and I were able to collect 93 numbers of Rubiaceae, representing 75 species, of which 20 are new to science.

Standley's "Rubiaceae of Ecuador" contains 178 species and 45 genera. According to Standley (in litt.) 56 new and undescribed species are represented in my Ecuadorian collections alone. This nearly equals one third of the known rubiaceous flora of Ecuador. With the addition of some 30 species from my collections which are already described but not previously known from Ecuador, the known rubiaceous flora is increased by half. It is probable that the addition of novelties from the collections of Camp, Wiggins, Drew, Prescott, and Ownbey will double or more than double the known Rubiaceae of Ecuador, and Dr. Standley has already expressed the intention of revising his "Rubiaceae of Ecuador" when all the collections from

our work have reached him. To avoid the publication of *nomina nuda*, Dr. Standley's proposed new species will not be mentioned here although included in the statistics. He has given names to new species in the following genera (the number in parentheses is the number of new species in that genus): *Cephaelis* (3), *Faramea* (4), *Hoffmannia* (3), *Holtonia* (1), *Manettia* (3), *Palicourea* (24), *Pentagonia* (1), *Psychotria* (14), *Rondeletia* (1), *Rustia* (1), and *Schradera* (1). Of these genera, *Holtonia*, *Rustia*, and *Schradera* are previously unreported from the Ecuadorian flora. I have already described a new species in the previously unreported genus *Joosia* (Steere 1943), and in the following list *Posoqueria*, *Chomelia*, and *Hemidiodia* were not heretofore known from Ecuador. The genus *Coccocypselium*, although not included in the "Rubiaceae of Ecuador," was later reported by Diels (1937).

In the following list of collections, geographic data are given in detail, in order that the origin of each specimen may be localized with some precision. Our work in Ecuador was hampered by the lack of accurate, large-scale maps of the regions which we explored, as well as by the lack of any sort of gazetteer, good or bad. The *Guía geográfica* and the excellent semi-topographic maps of each department, available in Colombia, were of great help there, both in planning explorations and in arriving at a common understanding on regions with land-owners and bark dealers, and I missed these aids when I moved from Colombia to Ecuador in July, 1943. The map of Ecuador published by Wolf in 1891, and distributed with his *Ecuador* (1892), is still the best in existence, even after more than fifty years. A useful, although reduced copy of it is easily available in Diels' work (1937). Later maps have all been copied from Wolf's, but in addition to including his errors, they have introduced new ones. The wall-map for schools prepared by Dr. Tuffiño and published under government sponsorship in 1925 is useful because of its large scale.

According to some official maps, the Río Pastaza serves to divide the Oriente of Ecuador into two provinces, Napo-Pastaza on the north and Santiago-Zamora on the south; according to others, the Río Huamboya is the division line. The two provinces are accepted fairly generally in Ecuador except at the division point itself, where no distinction whatever is made between Napo-Pastaza and Santiago-Zamora, and the whole region is simply called "Oriente." Consequently, to avoid a violation of present-day usage in Ecuador, "Prov. Napo-Pastaza" has been applied to the Oriente east of the northernmost provinces, and "Prov. Oriente" to that part east of the central provinces of Tungurahua and Chimborazo. The observance of this usage also serves the useful purpose of keeping separate in the list the collections from the northernmost part of the Oriente region, at the Colombian frontier, and those from the valley of the Río Pastaza of the central Oriente.



In the following list, the specimens are cited by provinces from North to South. This arrangement also happens to coincide rather closely with the chronological order in which the collections were made. All the specimens seen by Dr. Standley are contained in the Herbarium of the Chicago Natural History Museum. A full set belongs to the United States National Herbarium, and a third set will be placed in the Herbarium of the University of Michigan, Ann Arbor. A complete set of the specimens which I collected jointly with Dr. W. H. Camp, and a fourth set of my own collections will be deposited in the Herbarium of the New York Botanical Garden.

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### ECUADORIAN RUBIACEAE COLLECTED BY WILLIAM C. STEERE

**ARCYTOPHYLLUM ARISTATUM** Standl. PROV. CARCHI: Páramo above Tufiño, southeast slope of Volcán de Chiles, Cordillera Occidental, 12,000 ft. alt., Aug. 21, 1943, *Steere 8033, 8034*; Páramo de la Piedra, summit of Cordillera Oriental directly east of San Gabriel, 12,000 ft. alt., Oct. 21, 1943, *Steere 8122*. This species has already been reported from Carchi, as well as from the provinces of Azuay and Loja.

**ARCYTOPHYLLUM CAPITATUM** (Benth.) Schum. PROV. CARCHI: Páramo de la Piedra, very summit of Cordillera Oriental directly east of San Gabriel, 12,000 ft. alt., Oct. 21, 1943, *Steere 8121*. A shrub to 0.5 m. high with pink and lavender flowers; previously known from Ecuador without locality.

**ARCYTOPHYLLUM THYMIFOLIUM** (R. & P.) Standl. PROV. CARCHI: Roadside at Rumichaca (Ecuadorian-Colombian frontier), Interandean Valley just

north of Tulcán, 10,000 ft. alt., Oct. 3, 1943, *Steere 8090*. PROV. IMBABURA: Páramo de Pugarán, above Cahuasquí, west of Ibarra, Cordillera Occidental, 10,000 ft. alt., Dec. 13, 1943, *Steere 8194*. PROV. PICHINCHA: Dominant vegetation on arid slopes of steppe at kilometer 56 on Pan-American Highway south of Cayambe, Interandean Valley, 8000 ft. alt., Nov. 4, 1943, *Steere 8167*. PROV. TUNGARAHUA: Roadside just west of Pillaro, road to Ambato, Interandean Valley, 9000 ft. alt., Aug. 6, 1944, *Steere 8345*. The commonest species of *Arcytophyllum* in Ecuador, but not previously known from Carchi and Imbabura.

*BORRERIA LAEVIS* (Lam.) Griseb. PROV. CARCHI: Dry roadside, 5 kilometers east of Maldonado, Cordillera Occidental, 6000 ft. alt., Aug. 23, 1943, *Steere 8058*. PROV. IMBABURA: Along trail, Colonia Buenos Aires, west of Ibarra, Cordillera Occidental, 7500 ft. alt., Dec. 15, 1943, *Steere 8200*. PROV. LEÓN: Shaded bank, north side of Río Macuchi, near Esperanza, Cordillera Occidental, 5200 ft. alt., Sept. 8, 1943, *Steere 8077*. PROV. ORIENTE: Along trail near junction of Río Pastaza and Río Estancias, Cordillera Oriental, 4400 ft. alt., May 7, 1944, *Steere & Camp 8251*. A common tropical American weed not reported before from the highland provinces of Ecuador.

*BORRERIA OCIMOIDES* (Burm.) DC. PROV. CARCHI: Dry trailside, 5 kilometers east of Maldonado, Cordillera Occidental, 6000 ft. alt., Aug. 23, 1943, *Steere 8065*. PROV. ORIENTE: Along trail near Junction of Río Pastaza and Río Estancias, Cordillera Oriental, 4400 ft. alt., May 7, 1944, *Steere & Camp 8245, 8252*. A widely distributed tropical American weed previously known in Ecuador only from the province of Imbabura.

*CEPHAËLIS AXILLARIS* Sw. PROV. NAPO-PASTAZA: In deep wet forest above La Fama, Río Chingual, east of El Pun, Cordillera Oriental, 7200 ft. alt., Aug. 10, 1943, *Steere 8025*. This species has not been reported previously from Ecuador, although it is known from Colombia, Central America, and the West Indies.

*CEPHAËLIS JAMESONII* Standl. PROV. CARCHI: In deep forest below Tambo Jucal, west slope of Volcán de Chiles, Cordillera Occidental, 10,000 ft. alt., Aug. 22, 1943, *Steere 8039*; In deep forest on high ridge across Río Plata from Tambo la Palma, west slope of Volcán de Chiles, Cordillera Occidental, 9000 ft. alt., Oct. 6, 1943, *Steere 8093a*. PROV. IMBABURA: In dense forest above Colonia Buenos Aires on trail to La Cocha, Cordillera Occidental, 8500 ft. alt., Dec. 15, 1943, *Steere 8203*. This species has proved to be of considerable interest because it seems to be associated in general with *Cinchona pitayensis* Wedd., and is the best indicator species which I was able to find in the Cordillera Occidental of Ecuador. Since the type material of this *Cephaëlis* came from the western slope of Volcán de Pichincha, it was considered worthwhile to search there for *Cinchona pitayensis*, on the basis of the association noted in the northern provinces of Carchi and Imbabura. As already reported (*Steere 1944*), the *Cinchona* was found as predicted.

*CEPHAËLIS TOMENTOSA* (Aubl.) Vahl. PROV. ORIENTE: In roadside forest 10 kilometers east of Mera, foothills of Cordillera Oriental, 4000 ft. alt., May 11, 1944, *Steere & Camp 8276*. A common and widespread tropical American species which has been reported from Ecuador only from the province of El Oro, in the western range.

*CHOMELIA BARBELLATA* Standl. PROV. ORIENTE: In dense forest east of Puyo, on trail to Arajuno, Cordillera Oriental (foothills), 3000 ft. alt., May

12, 1944, *Steere & Camp 8290*. A Peruvian species not previously known from Ecuador.

*CINCHONA OFFICINALIS* L. PROV. NAPO-PASTAZA: In dense, wet forest above Río las Ollas, at junction with Río Chingual, Cordillera Oriental, 6250 ft. alt., Aug. 3, 1943, *Steere 8013*; On nearly vertical cuesta above Río Cofanes, at point called San Antonio, Cordillera Oriental, 7250 ft. alt., Oct. 23, 1943, *Steere 8134*. PROV. ORIENTE: In dense, wet forest, valley of Río Pastaza in zone of El Topo, Cordillera Oriental, 5500 ft. alt., May 2, 1944, *Steere & Camp 8226*; 4500 ft. alt., May 5, 1944, *Steere & Camp 8238*; 7000 ft. alt., May 10, 1944, *Steere & Camp 8271*; In deep, wet forest on flood-plain of Río Pastaza just south of Shell-Mera, May 13, 1944, 3500 ft. alt., *Steere & Camp 8300*. In Ecuador, this may be considered either a single extremely variable and complex species, or a group of reasonably distinct species or subspecies. For example, numbers 8226 and 8238 cited above represent a form with large, delicate leaves, whose bark is rich in alkaloids, giving an average of 1.5 per cent of quinine and an average of 4.5 per cent of total crystallizable alkaloids. Numbers 8013, 8134, and 8271 represent another form of higher altitudes, with much smaller leathery leaves, whose bark contains almost no quinine and a very low percentage (0.5–1.5) of total crystallizable alkaloids. In a critical revision of the genus, these will probably be considered as distinct species. This species (in the broad sense in which it is treated by Standley) has been known previously in Ecuador only from the province of Loja, in the southernmost part of the republic.

*CINCHONA PITAYENSIS* Wedd. PROV. CARCHI: On steep slopes, headwaters of Río la Plata, west slopes of Volcán de Chiles, Cordillera Occidental, 9770 ft. alt., Aug. 22, 1943, *Steere 8043*; 9700 ft. alt., Oct. 10, 1943, *Steere 8097*; Tambo Breñaña, above Río Bella Vista, 9000 ft. alt., Cordillera Oriental, Oct. 22, 1943, *Steere 8125*; Hacienda Indúgel, Interandean Valley directly east of San Gabriel, 9500 ft. alt., Oct. 27, 1943, *Steere 8153*. PROV. IMBABURA: Fila de Moinala, above Río Asabi, southwest slopes of Volcán de Cotacachi, Cordillera Occidental, 8500 ft. alt., Dec. 3, 1943, *Steere 8191*; Dense forest at headwaters of Río Rumichaca, old road between Colonia Buenos Aires and La Cocha, Cordillera Occidental west of Ibarra, 9500 ft. alt., Dec. 15, 1943, *Steere 8201*. The unsuspected existence of this species in Ecuador, its discovery, and its at present known distribution have been discussed at some length (*Steere 1944*). A curious feature of this species, now known well south of Quito, is that south of Pichincha, its alkaloid content drops markedly, and the bark contains very little quinine.

*CINCHONA PUBESCENS* Vahl. PROV. NAPO-PASTAZA: In clearing at Cesario, Río Chingual, Cordillera Oriental, 4750 ft. alt., Aug. 4, 1943, *Steere 8014*; At edge of clearing, Sebunday, Río Chingual, 6250 ft. alt., Aug. 9, 1943, *Steere 8023*. PROV. CARCHI: At Tambo Bella Vista on summit between Río la Plata and Río San Juan, west slope of Volcán de Chiles, Cordillera Occidental, 8400 ft. alt., Aug. 23, 1943, *Steere 8053*. PROV. IMBABURA: In plaza of Colonia Buenos Aires, Cordillera Occidental west of Ibarra, 7450 ft. alt., Dec. 14, 1943, *Steere 8195*. PROV. PICHINCHA: Roadside at about kilometer 45, Quito-Santo Domingo Road, Cordillera Occidental, Nov. 9, 1943, *Steere 8168*. PROV. LEÓN: Hacienda Nanaló, Macuchi Mines region, Cordillera Occidental, 5500 ft. alt., Sept. 8, 1943, *Steere 8080*. PROV. ORIENTE: On bank of Río Estancias near junction with Río Pastaza, El Topo region, Cordillera Oriental, 4000 ft. alt., May 2, 1944, *Steere & Camp 8225*; Roadside not far

west of Puyo, road to Shell-Mera, 3000 ft. alt., May 12, 1944, *Steere & Camp 8299*. This species seems to occur on the slopes of the Andes throughout Ecuador, although it does not seem to have been reported previously from the northern half of the republic. Except for a high-yielding race cultivated in the province of Bolívar, this species produces almost no quinine and rather low percentages of other alkaloids, mostly cinchonine.

*COCCOCYPSELUM CONDALIA* Pers. PROV. ORIENTE: On bank of Río Estancias near junction with Río Pastaza, region of El Topo, Cordillera Oriental, 4400 ft. alt., May 7, 1944, *Steere & Camp 8248*; Roadside bank not far west of Puyo, road to Shell-Mera, 3000 ft. alt., May 12, 1944, *Steere & Camp 8297*. This species has been reported from the same general region by Diels (1937) as *C. umbellatum* Poir.

*COFFEA ARABICA* L. As noted by Standley (1931), this important plant is widely cultivated in Ecuador; I have seen it in nearly every province.

*CONDAMINEA CORYMBOSA* (R. & P.) DC. PROV. NAPO-PASTAZA: Trail along Río Chingual, northwest of Cesario, Cordillera Oriental, 5000 ft. alt., Aug. 4, 1943, *Steere 8016*. PROV. CARCHI: Forest just east of Maldonado, Río San Juan, Cordillera Occidental, 5450 ft. alt., Aug. 23, 1943, *Steere 8060*. PROV. ORIENTE: On bank of Río Estancias near junction with Río Pastaza, region of El Topo, Cordillera Oriental, 4400 ft. alt., May 7, 1944, *Steere & Camp 8255*. Previously reported in Ecuador from Loja (Standley 1931) and from the Pastaza valley (Diels 1937).

*CORYNULA PILOSA* (Benth.) Hook. PROV. CARCHI: Roadside, Hacienda Indúgel, east of San Gabriel, Interandean Valley, 9000 ft. alt., Oct. 21, 1943, *Steere 8118*. PROV. IMBABURA: In meadow below Páramo de Taminanga, above Río Asabí, west slope of Volcán de Cotacachi, Cordillera Occidental, 9000 ft. alt., Dec. 2, 1943, *Steere 8188*. PROV. PICHINCHA: Páramo above Chillogallo, south slope of Volcán de Pichincha, 11,300 ft. alt., May 20, 1944, *Steere & Camp 8324*. This species has been known in Ecuador only from the type locality in the province of Pichincha.

*ELAEAGIA UTILIS* (Goudot) Wedd. PROV. CARCHI: In dense forest about 10 kilometers east of Maldonado, Río San Juan, Cordillera Occidental, 6500 ft. alt., *Steere 8069*. PROV. IMBABURA: In dense forest along Río Lita, below Colonia Buenos Aires, Cordillera Occidental west of Ibarra, 6500 ft. alt., Dec. 20, 1943, *Steere 8211*. PROV. ORIENTE: In dense, wet forest, valley of Río Pastaza in region of El Topo, Cordillera Oriental, 4750 ft. alt., May 5, 1944, *Steere & Camp 8240*. Although all these specimens are sterile, the plants from which they came resembled very closely true *Elaeagia utilis* which I have seen in Colombia. Furthermore, all these specimens bear the characteristic resinous gum in the upper nodes.

*FARAMEA COERULESCENS* Schum. & Krause. PROV. CARCHI: In forest below Tambo la Palma, headwaters of Río la Plata, west slope of Volcán de Chiles, Cordillera Occidental, 9500 ft. alt., Oct. 5, 1943, *Steere 8092*. Previously reported from the provinces of Azuay and Loja, in the southernmost part of Ecuador.

*FARAMEA MAYNENSIS* Spruce. PROV. ORIENTE: In dense forest, steep valley of Río Pastaza between El Topo and Baños, Cordillera Oriental, 5500 ft. alt., May 10, 1944, *Steere & Camp 8267*. Reported from Ecuador only from the province of Guayas.

*FARAMEA OBLONGIFOLIA* Standl. PROV. IMBABURA: In forest, Río Pamplona, Selva Alegre, west slope of Volcán de Cotacachi, Cordillera Occidental, 7000

ft. alt., Nov. 26, 1943, *Steere 8185*. A Colombian species not previously reported from Ecuador.

*GALIUM APARINE* L. PROV. CARCHI: Roadside, Hacienda Indúgel, Interandean Valley directly east of San Gabriel, 9000 ft. alt., Oct. 27, 1943, *Steere 8161*; Along trail just east of Huaca, 10,000 ft. alt., Oct. 31, 1943, *Steere 8164*; In clearing above Río La Mina, Colonia Huaqueña, 10,000 ft. alt., Nov. 1, 1943, *Steere 8166*. A cosmopolitan weed not reported from Ecuador until very recently (Acosta-Solis 1943) from the province of Pichincha.

*GALIUM CANESCENS* HBK. PROV. NAPO-PASTAZA: Side of trail along Río Chingual, between El Pun and Los Andes, Cordillera Oriental, 9500 ft. alt., July 31, 1943, *Steere 8005a, 8006*. PROV. CARCHI: On steep bank of Río Chiles, Tuffiño, Interandean Valley west of Tulcán, 10,700 ft. alt., Aug. 20, 1943, *Steere 8028*; Along trail below Tambo Jucal, west slope of Volcán de Chiles, Cordillera Occidental, 10,000 ft. alt., Aug. 22, 1943, *Steere 8042*; Trailing over roadside bank, Rumiehaca (Ecuadorian-Colombian frontier), Interandean Valley north of Tulcán, 10,000 ft. alt., Oct. 3, 1943, *Steere 8091*; Roadside, Hacienda Indúgel, east of San Gabriel, Interandean Valley, 9000 ft. alt., Oct. 21, 1943, *Steere 8119*. PROV. PICHINCHA: Páramo above Chillogallo, south slope of Volcán de Pichincha, Cordillera Occidental, 11,300 ft. alt., May 20, 1944, *Steere & Camp 8321*. PROV. LEÓN: On steep bank in forest above Pilaló, headwaters of Río Macuchi, Cordillera Occidental, 8500 ft. alt., Sept. 10, 1943, *Steere 8084*. Standley (1931) has cited five Ecuadorian specimens, all from the province of Pichincha.

*GALIUM PILIFERUM* HBK. PROV. CARCHI: On steep bank of Río Chiles, in village of Tuffiño, Interandean Valley west of Tulcán, 10,700 ft. alt., Aug. 20, 1943, *Steere 8028* (in part); Roadside at point called Salado, above El Pun, east of Tulcán, Cordillera Oriental, 9500 ft. alt., Oct. 15, 1943, *Steere 8105*. PROV. PICHINCHA: Páramo above Chillogallo, south slope of Volcán de Pichincha, Cordillera Occidental, 11,300 ft. alt., May 20, 1944, *Steere & Camp 8323*.

*GALIUM TETRAPLASIUM* Standl. PROV. CARCHI: On steep banks of Río Chiles, in village of Tuffiño, Interandean Valley west of Tulcán, 10,700 ft. alt., Aug. 20, 1943, *Steere 8029*. Not previously reported from Ecuador.

*GOMOZIA GRANADENSIS* L. (*Nertera depressa* Banks & Soland.) PROV. NAPO-PASTAZA: In trail along Río Chingual near Hacienda Macarenas, east of El Pun, Cordillera Oriental, alt. 9000 ft., July 29, 1943, *Steere 8002*; Bank of Río Alegría near junction with Río Chingual, 6140 ft. alt., Aug. 3, 1943, *Steere 8012*. PROV. CARCHI: On roadside bank in páramo between Tulcán and El Pun, Cordillera Oriental, 11,000 ft. alt., July 29, 1943, *Steere 8000*; October 15, 1943, *Steere 8102*; On rock near Tambo la Palma, headwaters of Río la Plata, west slope of Volcán de Chiles, Cordillera Occidental, 9000 ft. alt., Aug. 22, 1943, *Steere 8041*; Oct. 7, 1943, *Steere 8095*. PROV. PICHINCHA: Páramo above Chillogallo, south slope of Volcán de Pichincha, Cordillera Occidental, 11,300 ft. alt., May 20, 1944, *Steere & Camp 8318*. A very common plant which has not before been reported from the northernmost provinces. Numbers 8041 and 8095 are a form with juniper-like leaves and a very different manner of growth. I suspect that a critical revision of all material would result in the segregation of these specimens as a new species.

*GONZALAGUNIA CORNIFOLIA* (HBK.) Standl. PROV. ORIENTE: On bank, east of Puyo, trail to Canelos and Arajuno, foothills of Cordillera Oriental, 3000 ft. alt., May 12, 1944, *Steere & Camp 8296*. Already reported from the same general region by Diels (1937).

**GONZALAGUNIA DEPENDENS** R. & P. PROV. CARCHI: Roadside, Tambo Encanto, above Río la Plata, west slope of Volcán de Chiles, Cordillera Occidental, 8500 ft. alt., Aug. 26, 1943, *Steere 8073*; 5 kilometers east of Maldonado, Aug. 26, 1943, *Steere 8072*. PROV. ORIENTE: Bank of Río Estancias near junction with Río Pastaza, region of El Topo, Cordillera Oriental, 4400 ft. alt., May 7, 1944, *Steere & Camp 8253*; In forest, flood plain of Río Pastaza just south of Shell-Mera, 3500 ft. alt., May 13, 1944, *Steere & Camp 8300*. Previously reported only from the provinces of Loja and Pichincha, in Ecuador.

**GONZALAGUNIA RUDIS** Standl. PROV. ORIENTE: In dense forest in valley of Río Pastaza, region of El Topo, Cordillera Oriental, 4500 ft. alt., May 5, 1944, *Steere & Camp 8243*. A Panamanian and Colombian species not before reported from Ecuador.

**GONZALAGUNIA SORORIA** Standl. PROV. CARCHI: Below Tambo Bella Vista, west slope of Volcán de Chiles, Cordillera Occidental, 7000 ft. alt., Aug. 23, 1943, *Steere 8056*. PROV. IMBABURA: Trail above Selva Alegre, southwest slope of Volcán de Cotacachi, Cordillera Occidental, 10,000 ft. alt., Nov. 24, 1943, *Steere 8181*. PROV. ORIENTE: Bank of Río Estancias at junction with Río Pastaza, region of El Topo, Cordillera Oriental, 4400 ft. alt., May 7, 1944, *Steere & Camp 8254*. Previously known only from the type locality in the province of El Oro, Ecuador.

**GUETTARDA HIRSUTA** (R. & P.) Pers. PROV. CARCHI: Headwaters of Río la Plata, west slope of Volcán de Chiles, Cordillera Occidental, 9500 ft. alt., Aug. 22, 1943, *Steere 8045*. PROV. IMBABURA: Fila de Moinala, above Río Asabí, west slope of Volcán de Cotacachi, Cordillera Occidental, 9400 ft. alt., Dec. 3, 1943, *Steere 8190*; in dense ridge forest, trail between Colonia Buenos Aires and Guajara, Río Mira, Cordillera Occidental, 10,000 ft. alt., Dec. 18, 1943, *Steere 8207*. Previously known in Ecuador from a single specimen without locality.

**GUETTARDA SABICEOIDES** Standl. PROV. CARCHI: Chachasal, 8 kilometers south of El Pun, Cordillera Oriental, 9000 ft. alt., Oct. 19, 1943, *Steere 8115*; Nov. 10, 1943, *Steere 8180*. PROV. ORIENTE: Between Río Pastaza and road, El Topo, Cordillera Oriental, 4000 ft. alt., May 8, 1944, *Steere & Camp 8257*; In forest, Shell-Mera, 3500 ft. alt., May 11, 1944, *Steere & Camp 8280*; Along trail, not far west of Puyo, 3000 ft. alt., May 12, 1944, *Steere & Camp 8287*. A Colombian species not previously reported from Ecuador.

**HAMELIA PATENS** Jacq. PROV. LEÓN: On bank of Río Macuchi just below electric plant for Macuchi Mines, 3500 ft. alt., Sept. 11, 1943, *Steere 8089*. A common and widespread tropical American species reported from several Ecuadorian provinces, but not previously from León.

**HAMELIA PEDICELLATA** Wernham. PROV. ORIENTE: On east bank of Río Puyo, across from village of Puyo, foothills of Cordillera Oriental, 3000 ft. alt., May 12, 1944, *Steere & Camp 8292*. Previously reported in Ecuador only from the province of Guayas.

**HEMIDIODIA OCIMIFOLIA** (Willd.) Schum. PROV. IMBABURA: Along trail, Río Mira near junction with Río Lita, Cordillera Occidental, 2000 ft. alt., Nov. 22, 1943, *Steere 8215*. A common weed in tropical America which by some accident does not seem to have been reported from Ecuador.

**HILLIA PARASITICA** Jacq. PROV. CARCHI: Creeping over bank along trail, just below Tambo Bella Vista, Río San Juan, Cordillera Occidental, 8300 ft. alt., Aug. 26, 1943, *Steere 8070*. PROV. IMBABURA: On steep hillside, Río

Lita below Colonia Buenos Aires; Cordillera Occidental west of Ibarra, 7000 ft. alt., Dec. 14, 1943, *Steere 8196*. Previously known in Ecuador only from a Spruce specimen without locality data.

*HOFFMANNIA ECUATORIANA* Standl. PROV. ORIENTE: In deep, wet forest, valley of Río Pastaza, region of El Topo, Cordillera Oriental, 4400 ft. alt., May 4, 1944, *Steere & Camp 8230*. This specimen was collected in the same general zone as the type specimen and is a very conspicuous species because of the bright, China-red flowers. It has been collected and reported from this region also by Diels.

*HOFFMANNIA SPRUCEI* Standl. PROV. NAPO-PASTAZA: Along stream, near La Fama, Río Chingual, Cordillera Oriental, 7000 ft. alt., Aug. 2, 1943, *Steere 8011*. PROV. CARCHI: At bridge over Río Bella Vista half day from junction with Río Cofanes, Cordillera Oriental east of San Gabriel, 8050 ft. alt., Oct. 22, 1943, *Steere 8128*. PROV. LEÓN: In deep, wet forest, Hacienda Nanaló, Macuchi Mines region, Cordillera Occidental, 5500 ft. alt., Sept. 8, 1943, *Steere 8083*. Previously reported from one specimen without locality data.

*ISERTIA ALBA* Sprague. PROV. ORIENTE: On bank of Río Estancias near junction with Río Pastaza, region of El Topo, Cordillera Oriental, 4400 ft. alt., May 7, 1944, *Steere & Camp 8217*. This is a common and abundant tree in the valley of the Río Pastaza, but has not been reported from Ecuador. However, in view of its occurrence in Colombia and Peru, its discovery in Ecuador is not surprising.

*ISERTIA PITTIERI* (Standl.) Standl. PROV. IMBABURA: Forest along Río Mira, near junction with Río Lita, Cordillera Occidental, 2000 ft. alt., Nov. 22, 1943, *Steere 8221*. A Colombian species not previously known from Ecuador.

*JOOSIA PULCHERRIMA* Steere. PROV. NAPO-PASTAZA: In wet, mossy forest above Río Garrapatera, east of La Bonita, Río Chingual, Cordillera Oriental, 7000 ft. alt., Aug. 6, 1943, *Steere 8018*; In wet forest above La Fama, Río Chingual, 7200 ft. alt., Aug. 10, 1943, *Steere 8026*. PROV. CARCHI: Common in dense forest along Río Bella Vista several hours above its junction with Río Cofanes, Cordillera Oriental, 8000 ft. alt., Oct. 22, 1943, *Steere 8129*. The last specimen cited here was not mentioned in the original description of the species (Steere 1943) because the manuscript was already in the hands of the printer at the time 8129 was collected.

*LADENBERGIA MACROCARPA* (Vahl) Klotzsch. PROV. NAPO-PASTAZA: In deep forest, valley of Río Chingual east of El Pun, Cordillera Oriental, 9000 ft. alt., July 29, 1943, *Steere 8004*. PROV. CARCHI: At Tambo Encanto, Río la Plata, west slope of Volcán de Chiles, Cordillera Occidental, 8700 ft. alt., Aug. 22, 1943, *Steere 8048*; Below El Pun, toward Río Chingual, Cordillera Oriental, 9000 ft. alt., Oct. 16, 1943, *Steere 8108*. Reported only from the southernmost provinces of Loja and Azuay.

*LADENBERGIA MAGNIFOLIA* (R. & P.) Klotzsch. PROV. NAPO-PASTAZA: In clearing at Cesario, Río Chingual, Cordillera Oriental, 4750 ft. alt., Aug. 4, 1943, *Steere 8015*. PROV. CARCHI: In forest, about 10 kilometers east of Maldonado, Río San Juan, Cordillera Occidental, 6780 ft. alt., August 23, 1943, *Steere 8059*. I have attached this name to specimens which occur at and below the zone of *Cinchona pubescens* and which, as in Colombia, have hollow twigs.

**MACROCNEUM SPRUCEI** Rusby. PROV. NAPO-PASTAZA: Deep forest above La Fama, Río Chingual, Cordillera Oriental, 7000 ft. alt., Aug. 2, 1943, *Steere 8008*. A Bolivian species not before reported from Ecuador.

**MANETTIA ECHITIDEA** Standl. PROV. CARCHI: In tree along trail just east of Huaca, Interandean Valley, 10,000 ft. alt., Oct. 31, 1943, *Steere 8162*. Previously reported from Ecuador only from the province of Pichincha.

**MANETTIA EVENIA** Sprague. PROV. CARCHI: In forest on high ridge between Río Bella Vista and Río Tigre Chico, both tributaries of Río Cofanes, Cordillera Oriental, 9000 ft. alt., Oct. 24, 1943, *Steere 8143*; Hacienda Indúgel, Interandean Valley directly east of San Gabriel, 9000 ft. alt., Oct. 27, 1943, *Steere 8155*. Previously reported from Ecuador from the province of Pichincha.

**MANETTIA FLEXILIS** Brandeg. PROV. CARCHI: Bank of Río la Plata near junction with Río San Juan, just east of Maldonado, Cordillera Occidental, 5200 ft. alt., *Steere 8068*. Otherwise known in Ecuador only from the province of Chimborazo.

**MANETTIA PICHINCHENSIS** Wernham. PROV. PICHINCHA: Páramo above Chillogallo, south slope of Volcán de Pichincha, Cordillera Occidental, 11,300 ft. alt., May 20, 1944, *Steere & Camp 8322*. This species is known only from Pichincha, but many collections have been made there.

**MANETTIA RACEMOSA** R. & P. PROV. ORIENTE: Among shrubs, bank of Río Estancias at its junction with Río Pastaza, region of El Topo, Cordillera Oriental, 4400 ft. alt., May 7, 1944, *Steere & Camp 8250*. A Peruvian species, not before reported from Ecuador.

**MANETTIA RECURVA** Sprague. PROV. CARCHI: In forested ravine at very edge of páramo, Tambo Jucal, west slope of Volcán de Chiles, Cordillera Occidental, 11,100 ft. alt., Aug. 21, 1943, *Steere 8037*; At edge of forest, Tambo Encanto, 8700 ft. alt., Aug. 22, 1943, *Steere 8050*; Hacienda Indúgel, Interandean Valley directly east of San Gabriel, 9000 ft. alt., Oct. 27, 1943, *Steere 8154*. These are apparently the first collections from the northern half of Ecuador.

**MANETTIA SKUTCHII** Standl. PROV. ORIENTE: On shrub several kilometers west of Puyo, road to Shell-Mera, foothills of Cordillera Oriental, 3000 ft. alt., May 12, 1944, *Steere & Camp 8284*; On tree, several kilometers east of Puyo, trail to Arajuno and Canelos, May 12, 1944, *Steere & Camp 8291*; Roadside just west of Shell-Mera, May 13, 1944, *Steere & Camp 8317*. According to Standley (in litt.), "This species has been known heretofore only from the original collection," which was made in 1939 in the same general region.

**MANETTIA TRIANAE** Wernham. PROV. CARCHI: Chorrera de la Loma Rinconada, south of El Pun, Cordillera Occidental, 9000 ft. alt., Oct. 19, 1943, *Steere 8117*. This is the first report from the northern half of Ecuador; otherwise known from the province of Tungurahua.

**PALICOUREA ANGUSTIFOLIA** HBK. PROV. CARCHI: Chachasal, 8 kilometers south of El Pun, Cordillera Oriental, 9000 ft. alt., Oct. 19, 1943, *Steere 8116*; In dense forest above Río Bella Vista, a tributary of Río Cofanes, Cordillera Oriental, 8000 ft. alt., Oct. 22, 1943, *Steere 8131*; 7500 ft. alt., Oct. 24, 1943, *Steere 8140*. PROV. IMBABURA: Dense forest above Río Asabi, north side, west slope of Volcán de Cotacachi, Cordillera Occidental, 8500 ft. alt., Dec. 2, 1943, *Steere 8189*. PROV. ORIENTE: Dense forest, headwaters of Río Tigre, which joins Río Pastaza at El Topo, Cordillera Oriental, 5000 ft. alt., May



8, 1944, *Steere & Camp 8261*. A beautiful species definitely known previously in Ecuador only from the province of Tungurahua.

*PALICOUREA BALNEARIA* Standl. PROV. NAPO-PASTAZA: In deep forest, valley of Río Chingual near Hacienda Macarenas, east of El Pun, Cordillera Oriental, 9000 ft. alt., July 29, 1943, *Steere 8003*. This species has been known apparently only from the type locality, in the province of Tungurahua.

*PALICOUREA CALANTHA* Standl. PROV. LEÓN: In dense forest, Hacienda Nanaló, region of Macuchi Mines, Cordillera Occidental, 5500 ft. alt., Sept. 8, 1943, *Steere 8079*. The previously known distribution of this species in Ecuador has been in the province of Pichincha, the type locality.

*PALICOUREA CALDASANA* Standl. PROV. CARCHI: Loma Breñaña, Mirador, southeast of El Pun, Cordillera Oriental, 10,000 ft. alt., Oct. 18, 1943, *Steere 8113*; In forest along Río Bella Vista, headwaters of Río Cofanes, Cordillera Oriental, 8000 ft. alt., Oct. 22, 1943, *Steere 8130*. A Colombian species, not previously reported from Ecuador.

*PALICOUREA CALOTHYRSUS* Schum. & Krause. PROV. LEÓN: In dense forest above Pilaló, headwaters of Río Macuchi, Cordillera Occidental, 8500 ft. alt., Sept. 10, 1943, *Steere 8088*. Although several collections of this species have been reported from Ecuador, it has not apparently been collected previously in this particular province.

*PALICOUREA CHIMBORACENSIS* Standl. PROV. CARCHI: On bank of Río San Juan, just west of Maldonado, Cordillera Occidental, 5000 ft. alt., Aug. 24, 1943, *Steere 8066*. This species has been known heretofore only from the type locality, "at the foot of Mt. Chimborazo."

*PALICOUREA CROCEA* (Sw.) R. & S. PROV. CARCHI: In forest on terrace of Río San Juan, just east of Madonado, Cordillera Occidental, 5460 ft. alt., Aug. 23, 1943, *Steere 8064*. PROV. IMBABURA: In forest, Plaza de Selva Alegre, southwest slope of Volcán de Cotacachi, Cordillera Occidental, 4500 ft. alt., Nov. 28, 1943, *Steere 8186*. A widely distributed tropical American species, not previously reported from Ecuador.

*PALICOUREA EGENA* Standl. PROV. CARCHI: In forest, Hacienda Indúgel, Interandean Valley directly east of San Gabriel, 9000 ft. alt., Oct. 27, 1943, *Steere 8157*; In forest along trail, just east of Huaca, 10,000 ft. alt., Oct. 31, 1943, *Steere 8163*. The only collection of this species reported from Ecuador is from "Province of Pasto" (Standley 1931). Since the old province of Pasto, or Nariño, has had very flexible boundaries, it is difficult to know if Jameson's specimen came from present-day Ecuador, or from Colombia.

*PALICOUREA FLAVESCENS* HBK. PROV. CARCHI: In forest above Río Bella Vista, headwaters of Río Cofanes, Cordillera Oriental, 8500 ft. alt., Oct. 26, 1943, *Steere 8148*. Previously reported from the province of Carchi on the basis of a Lehmann specimen from "Mt. Tulcán."

*PALICOUREA GUIANENSIS* Aubl. PROV. ORIENTE: On terrace above Río Estancias near junction with Río Pastaza, region of El Topo, Cordillera Oriental, 4400 ft. alt., May 7, 1944, *Steere & Camp 8249*. Previously known in Ecuador from the provinces of El Oro and Chimborazo.

*PALICOUREA HOLMGRENII* Standl. PROV. CARCHI: In forest above Hacienda Indúgel, Interandean Valley directly east of San Gabriel, 9500 ft. alt., Oct. 21, 1943, *Steere 8120*. Previously known in Ecuador only from the type locality in the province of Pichincha.

*PALICOUREA HOSPITALIS* Standl. PROV. IMBABURA: Dense forest along trail above Selva Alegre, southwest slope of Volcán de Cotacachi, Cordillera Occi-

dental, 9000 ft. alt., Nov. 24, 1943, *Steere 8182*. PROV. ORIENTE: In dense, wet forest at headwaters of Río Tigre, which joins Río Pastaza at El Topo, Cordillera Oriental, 5300 ft. alt., May 9, 1944, *Steere & Camp 8263*; In dense, wet forest on high ridge between El Topo and Baños, 7500 ft. alt., May 10, 1944, *Steere & Camp 8272*; On bank of small stream just west of Shell-Mera, 3600 ft. alt., May 13, 1944, *Steere & Camp 8316*. This species has been known previously only from the type locality in southern Ecuador.

*PALICOUREA HUIGRENSIS* Standl. PROV. CARCHI: In forest, Tambo la Palma, headwaters of Río la Plata, west slope of Volcán de Chiles, Cordillera Occidental, 9500 ft. alt., Oct. 5, 1943, *Steere 8086, 8092a*; In forest above El Pun, east of Tulcán, Cordillera Oriental, 9000 ft. alt., Oct. 16, 1943, *Steere 8107*. Known previously only from the type locality in the province of Chimborazo and from Azuay.

*PALICOUREA KALBREYERI* Standl. PROV. CARCHI: Río Chingual at Sebunday, Cordillera Oriental, 6200 ft. alt., Nov. 6, 1943, *Steere 8174*. A Colombian species, not reported from Ecuador before.

*PALICOUREA LASIANTHA* Krause. PROV. ORIENTE: In dense, wet forest, headwaters of Río Tigre, which joins Río Pastaza at El Topo, Cordillera Oriental, 5300 ft. alt., May 9, 1943, *Steere & Camp 8264*. This appears to be the first definitely known locality in Ecuador, as Standley (1931) reports only a Pearce specimen from "Andes."

*PALICOUREA LEVIS* Standl. PROV. CARCHI: In forest at Tambo Encanto, headwaters of Río La Plata, west slope of Volcán de Chiles, Cordillera Occidental, 8700 ft. alt., Aug. 22, 1943, *Steere 8049*; In forest above Hacienda Indúgel, Interandean Valley directly east of San Gabriel, 9000 ft. alt., Oct. 27, 1943, *Steere 8156, 8158*. Standley cites three specimens, but from no locality north of Quito.

*PALICOUREA LUGUBRIS* Schum. & Krause. PROV. IMBABURA: In forest along Río Mira near junction with Río Lita, Cordillera Occidental, 2000 ft. alt., Nov. 22, 1943, *Steere 8222*. PROV. ORIENTE: In forest along trail between Shell-Mera and Puyo, perhaps 5 kilometers east of Shell-Mera, foothills of Cordillera Oriental, 3000 ft. alt., May 12, 1944, *Steere & Camp 8286*. Not previously reported from either province cited here.

*PALICOUREA OREADIUM* Standl. PROV. CARCHI: In last bit of forest at edge of páramo, Tambo Jucal, west slope Volcán de Chiles, Cordillera Occidental, 11,100 ft. alt. Aug. 21, 1943, *Steere 8036*; Below Tambo Jucal, 10,000 ft. alt., Aug. 22, 1943, *Steere 8038*; In forest above El Pun, east of Tulcán, Cordillera Oriental, 10,000 ft. alt., Oct. 15, 1943, *Steere 8103, 8104*; Terrace of Río Chingual, below El Pun, 9000 ft. alt., Oct. 16, 1943, *Steere 8109*; In forest just at tree line, below Páramo de la Piedra, Cordillera Oriental, 11,000 ft. alt., Oct. 21, 1943, *Steere 8123*; 10,500 ft. alt., Oct. 22, 1943, *Steere 8124*; 9000 ft. alt., *Steere 8126*; In forest above Río Bella Vista, headwaters of Río Cofanes, 9000 ft. alt., Oct. 24, 1943, *Steere 8141*; In forest above Hacienda Indúgel, Interandean Valley directly east of San Gabriel, 10,500 ft. alt., Oct. 27, 1943, *Steere 8152*. This species has previously been known from the type locality, in southern Ecuador.

*PALICOUREA PASTI* Wernham. PROV. CARCHI: In forest above Hacienda Indúgel, Interandean Valley directly east of San Gabriel, 9000 ft. alt., Oct. 27, 1943, *Steere 8159*. The previous reports of this species in Ecuador give no locality data.

**POSOQUERIA LATIFOLIA** (Rudge) R. & S. PROV. NAPO-PASTAZA: In forest, Las Ollas, Río Chingual, Cordillera Oriental, 6500 ft. alt., Nov. 7, 1943, *Steere 8175*. A common enough species in Colombia and Peru, but not before reported from Ecuador.

**PSYCHOTRIA BRACHIATA** Sw. PROV. ORIENTE: In dense, wet forest, valley of Río Pastaza, region of El Topo, Cordillera Oriental, 4400 ft. alt., May 4, 1944, *Steere & Camp 8233*; 4750 ft. alt., May 5, 1944, *Steere & Camp 8242*; In forest at Shell-Mera, 3500 ft. alt., May 11, 1944, *Steere & Camp 8279*. Apparently known otherwise in Ecuador only from the southernmost region currently in dispute between Ecuador and Peru.

**PSYCHOTRIA BULLATIFOLIA** Standl. PROV. ORIENTE: In dense, wet forest, flood plain of Río Pastaza, just south of Shell-Mera, foothills of Cordillera Oriental, 3500 ft. alt., May 13, 1944, *Steere & Camp 8307*. A Peruvian species, new for Ecuador.

**PSYCHOTRIA CUSPIDATA** Bredem. PROV. NAPO-PASTAZA: In deep forest, trail between Cesario and La Bonita, Río Chingual near junction with Río Sucio. Cordillera Oriental, 6000 ft. alt., Aug. 7, 1943, *Steere 8019*. Widely distributed in tropical America, but not previously reported from Ecuador.

**PSYCHOTRIA HARTWEGIANA** Standl. PROV. CARCHI: In forest, slopes of El Mirador, southeast of El Pun, Cordillera Oriental, 10,000 ft. alt., Oct. 17, 1943, *Steere 8112*; Above Tambo Breñaña, headwaters of Río Cofanes, Cordillera Oriental, 10,500 ft. alt., Oct. 27, 1943, *Steere 8151*; In forest above Huaca, to the east, Interandean Valley, 11,000 ft. alt., Oct. 31, 1943, *Steere 8165*. Although reported from Colombia and Bolivia, this species has not been known in Ecuador before.

**PSYCHOTRIA HIRTA** Humb. & Bonpl. PROV. CARCHI: In dense, wet, virgin forest across Río Plata from Tambo La Palma, west slope of Volcán de Chiles, Cordillera Occidental, 9000 ft. alt., Oct. 6, 1943, *Steere 8093*; In deep forest, nearly vertical cuesta above Río Cofanes, Cordillera Oriental, 7250 ft. alt., Oct. 23, 1943, *Steere 8135*. Standley does not report this species from Ecuador.

**PSYCHOTRIA JAMESONIANA** Standl. PROV. ORIENTE: In deep forest on steep ridge between El Topo and Baños, valley of Río Pastaza, Cordillera Oriental, 6000 ft. alt., May 10, 1944, *Steere & Camp 8268*. This species is not included in the "Rubiaceae of Ecuador."

**PSYCHOTRIA LATEMIFLORA** Standl. PROV. CARCHI: In wet forest above Tambo Breñaña, headwaters of Río Cofanes, Cordillera Oriental, 10,000 ft. alt., Oct. 27, 1943, *Steere 8150*. A Colombian species, not previously reported from Ecuador.

**PSYCHOTRIA MACROPHYLLA** R. & P. PROV. NAPO-PASTAZA: In deep virgin forest, Sebundoy, Río Chingual, Cordillera Oriental, 6300 ft. alt., Aug. 9, 1943, *Steere 8022*. PROV. CARCHI: In forest along trail between Tambo Bella Vista and Maldonado, west slope Volcán de Chiles, Cordillera Occidental, 7500 ft. alt., Aug. 23, 1943, *Steere 8054*; 5450 ft. alt., *Steere 8061*; In deep, wet forest across Río la Plata from Tambo la Palma, 9000 ft. alt., Oct. 6, 1943, *Steere 8094*; In forest above Río Bella Vista, headwaters of Río Cofanes, Cordillera Oriental, 8000 ft. alt., Oct. 22, 1943, *Steere 8132*. PROV. IMBABURA: In forest, Fila de Moinala, above Río Asabí, west slope Volcán de Cotacachi, Cordillera Occidental, 9400 ft. alt., Dec. 3, 1943, *Steere 8192*. PROV. LEÓN: In deep, wet forest, Hacienda Nanaló, Macuchi Mines region, Cordillera Occidental, 5500 ft. alt., Sept. 8, 1943, *Steere 8081*; above Pilaló,

headwaters of Río Macuchi, 8500 ft. alt., Sept. 10, 1943, *Steere 8085*. PROV. ORIENTE: Dense, wet forest, valley of Río Pastaza, region of El Topo, Cordillera Oriental, 4400 ft. alt., May 4, 1944, *Steere & Camp 8232*; In forest, headwaters of Río Tigre, which joins Río Pastaza at El Topo, 5400 ft. alt., May 9, 1944, *Steere & Camp 8265*; In deep wet forest on flood plain of Río Pastaza just south of Shell-Mera, foothills of Cordillera Oriental, 3500 ft. alt., May 13, 1944, *Steere & Camp 8304, 8305, 8314*. A common, abundant, and apparently extremely variable species in Ecuador. It has been reported with certainty only from the provinces of Guayas and Pichincha (Standley 1931).

PSYCHOTRIA PATENS SW. PROV. IMBABURA: In forest along Río Mira, near junction with Río Lita, Cordillera Occidental, 2000 ft. alt., Nov. 22, 1943, *Steere 8214*. Widely distributed in tropical America, but not reported previously from Ecuador.

PSYCHOTRIA PILOSA R. & P. PROV. ORIENTE: On bank of Río Estancias near junction with Río Pastaza, region of El Topo, Cordillera Oriental, 4400 ft. alt., May 7, 1944, *Steere & Camp 8256*; In forest at Shell-Mera, foothills of Cordillera Oriental, 3500 ft. alt., May 11, 1944, *Steere & Camp 8282*; In forest just east of Puyo, on trail to Arajuno and Canelos, 3000 ft. alt., May 12, 1944, *Steere & Camp 8293*; In dense, wet forest on flood-plain of Río Pastaza, just south of Shell-Mera, 3500 ft. alt., May 13, 1944, *Steere & Camp 8306*. A Peruvian and Bolivian species not previously reported from Ecuador.

PSYCHOTRIA RECORDIANA Standl. PROV. LEÓN: In deep forest, Hacienda Nanaló, Macuchi Mines region, Cordillera Occidental, 5500 ft. alt., Sept. 8, 1943, *Steere 8082*. This species is known otherwise only from the type locality in the parallel valley of the Río Saloya, Provincia de Pichincha, just to the north.

PSYCHOTRIA RIMBACHII Standl. PROV. IMBABURA: In forest along Río Mira, near junction with Río Lita, Cordillera Occidental, 2000 ft. alt., Nov. 22, 1943, *Steere 8213, 8218*. This species was not included by Standley in his "Rubiaceae of Ecuador" (1931).

PSYCHOTRIA RUFESCENS H. & B. PROV. IMBABURA: In forest along Río Mira, near junction with Río Lita, Cordillera Occidental, 2000 ft. alt., Nov. 22, 1943, *Steere 8217*. Previously reported in Ecuador only from the coast.

PSYCHOTRIA TENUIFOLIA SW. PROV. ORIENTE: In wet forest east of Shell-Mera, trail to Puyo, foothills of Cordillera Oriental, 3000 ft. alt., May 12, 1944, *Steere & Camp 8285*. Concerning this collection, Standley says (in litt.) "A species common in Central America and the West Indies, but not recorded for South America. I can not find any character for separating the Ecuadorian plant."

RELBUNUM CILIATUM (R. & P.) Hemsl. PROV. PICHINCHA: Páramo above Chillogallo, south slope of Volcán de Pichincha, Cordillera Occidental, 11,300 ft. alt., May 20, 1944, *Steere & Camp 8319*. A species widely distributed in Ecuador.

RELBUNUM HIRSUTUM (R. & P.) Schum. PROV. CARCHI: On steep bank of Río Chiles, in village of Tufiño, Interandean Valley west of Tulcán, 10,700 ft. alt., Aug. 20, 1943, *Steere 8030*; Among sedges in pure páramo, west slope of Volcán de Chiles, Cordillera Occidental, 13,000 ft. alt., Aug. 27, 1943, *Steere 8075*; In páramo above El Pun, east of Tulcán, 11,500 ft. alt., Oct. 15, 1943, *Steere 8099*; Roadside, Hacienda Indúgel, Interandean Valley directly

east of San Gabriel, 9000 ft. alt., Oct. 27, 1943, *Steere 8160*. Previously reported from Carchi on the basis of a specimen collected by Hitchcock.

*RELBUNUM HYPOCARPIUM* (L.) Hemsl. PROV. CARCHI: In fencerow above Tufiño, Interandean Valley west of Tulcán, 11,000 ft. alt., Aug. 21, 1943, *Steere 8032*; Along trail below Tambo Jucal, west slope Volcán de Chiles, Cordillera Occidental, 10,000 ft. alt., Aug. 22, 1943, *Steere 8040*; Tambo Bella Vista, 8400 ft. alt., Aug. 23, 1943, *Steere 8052*; In páramo above El Pun, east of Tulcán, Cordillera Oriental, 11,500 ft. alt., Oct. 15, 1943, *Steere 8100, 8101*; 9000 ft. alt., Oct. 16, 1943, *Steere 8106*. PROV. IMBABURA: In abandoned clearing above Colonia Buenos Aires, trail from Ibarra, Cordillera Occidental, 8000 ft. alt., Dec. 15, 1943, *Steere 8202*. PROV. LEÓN: On shaded bank, north side Río Macuchi, at Esperanza, Cordillera Occidental, 5200 ft. alt., Sept. 8, 1943, *Steere 8076*. PROV. ORIENTE: On bank of Río Estancias near junction with Río Pastaza, region of El Topo, Cordillera Oriental, 4400 ft. alt., May 7, 1944, *Steere & Camp 8244*.

*RELBUNUM NITIDUM* (HBK.) Schum. PROV. NAPO-PASTAZA: In trail near Hacienda Macarenas, valley of Río Chingual east of El Pun, Cordillera Oriental, 9000 ft. alt., July 29, 1943, *Steere 8001*. PROV. PICHINCHA: Páramo above Chillo Gallo, south slope of Volcán de Pichincha, Cordillera Occidental, 11,300 ft. alt., May 20, 1944, *Steere & Camp 8320*. The first specimen cited here extends the range in Ecuador considerably; the second comes from the general type locality.

*RONDELETIA TRICHOTOMA* Standl. PROV. ORIENTE: At edge of forest, high ridge between El Topo and Baños, 6000 ft. alt., May 10, 1943, *Steere & Camp 8275*. Since this specimen was collected in full view of the snows of Volcán de Tungurahua, it may be considered as being from the general type locality.

*RUDGEA CORNIFOLIA* (H. & B.) Standl. [*R. fimbriata* (Benth.) Standl.] PROV. ORIENTE: In dense, wet forest, valley of Río Pastaza, region of El Topo, Cordillera Oriental, 4400 ft. alt., May 4, 1944, *Steere & Camp 8235*. Previously reported only from coastal Ecuador.

*SABICEA PARAENSIS* (Schum.) Wernham. PROV. ORIENTE: In forest at Shell-Mera, foothills of Cordillera Oriental, 3500 ft. alt., May 11, 1944, *Steere & Camp 8278*; On bank just west of Puyo, trail to Shell-Mera, 3000 ft. alt., May 12, 1944, *Steere & Camp 8298*. An Amazonian and Peruvian species which has not previously been collected in Ecuador, to my knowledge.

*SABICEA VILLOSA* R. & S. PROV. IMBABURA: In forest along Río Mira, near junction with Río Lita, Cordillera Occidental, 2000 ft. alt., Nov. 22, 1943, *Steere 8216*. PROV. ORIENTE: Bank of Río Estancias near junction with Río Pastaza, region of El Topo, Cordillera Oriental, 4400 ft. alt., May 7, 1944, *Steere & Camp 8246*; In forest, Shell-Mera, foothills of Cordillera Oriental, 3500 ft. alt., May 11, 1944, *Steere & Camp 8277*. Previously known in Ecuador only from the western slopes.

DEPARTMENT OF BOTANY, UNIVERSITY OF MICHIGAN  
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**"EUPHORBIA CHAMAESYCE" IN THE UNITED STATES**

LEON CROIZAT

The very name of *Euphorbia Chamaesyce* L.<sup>1</sup> has been practically unknown to American taxonomists until the publication of Wheeler's recent monograph on *Euphorbia* L. subg. *Chamaesyce*. In this work Wheeler records this species for eleven States ranging from Massachusetts to Arizona (Rhodora **43**: 265. 1941), and offers the following elucidation (p. 269, 270), "Customarily the name *E. Chamaesyce* is applied to an entity native in the Mediterranean region and eastward into Asia. . . . There seems to be only one author, Swartz, Obs. Bot. Pl. Ind. Occ. 196. 1791, who has applied the name to any New World plant and this was ignored as a mere casual misapplication. However, while browsing through the specimens at the Field Museum, Chicago, in Sept., 1939, I came upon a photograph of the specimen in the Linnaean herbarium and fragments from the same specimen. . . . There is no doubt that *E. Chamaesyce*, as represented in the Linnaean herbarium, is identical with *E. prostrata* as usually interpreted. . . . One of the fundamental rules to be followed in the typification of a Linnaean species is that the Linnaean specimen is to be taken as type, except in extraordinary cases, if he had it in his herbarium at the time the species in question was published and if it conforms to his diagnosis. Exceptional cases are rare and require a full and elaborate explanation to establish acceptable grounds for refusing to accept the Linnaean specimen as type." On the strength of these findings and opinions, Wheeler treats as *E. Chamaesyce* L. Sp. Pl. **1**: 455 (1753) the entity commonly known as *E. prostrata* Ait. Hort. Kew. **2**: 139 (1789), stating: TYPE [of *E. Chamaesyce*]: Jamaica, *P. Browne* (Linnaean Herb. . . .) . . . TYPE [of *E. prostrata*]: "*Nat(ive)* of the West Indies. *Cult.* 1758, by Mr. Philip Miller" (British Museum if extant).

The purpose of these brief notes is to furnish the "full and elaborate explanation" which establishes the fact that the interpretation advanced in the quoted text is unacceptable, and must be rejected. Whether the Chicagoan fragment seen by Wheeler is authentic or not this writer does not profess to know.

The name *E. Chamaesyce* has universally been applied from 1753 to 1941 to an entity native to Europe, Africa and Western Asia. Likewise, the name *E. prostrata* has been generally given between 1862 and 1941 to a pandemic

<sup>1</sup> The species in this affinity are treated by the writer under *Chamaesyce* S. F. Gray emend. Croiz., as a distinct genus. To avoid unnecessary nomenclatural burdens in this brief comment, they are being referred here as *Euphorbia*.

tropical and subtropical weed. In the span of time mentioned these two entities have been taken up, in their classic sense, by thousands of authors, and have found their way into *tens of thousands* of publications. Lest this writer be suspected of exaggeration in speaking of tens of thousands of records, the reader may here be reminded of the fact that *every contribution* concerned with the plants of Europe, Africa, Asia, Oceania and America has used these two binomials in their traditional application, the exceptions being perhaps to be counted on the fingers of one hand to 1941.

If Wheeler's understanding of *E. Chamaesyce* and *E. prostrata* comes to pass, everyone of these records is automatically turned into a misapplication and falls into synonymy. The practical task that is to face the coming monographer of *Euphorbia* and its segregates in unravelling this fabulous synonymy is better left without comment. It is to be taken for certain that everybody in Europe, Africa, and Asia will continue to abide by the traditional applications of *E. Chamaesyce* and *E. prostrata* either by choice or necessity. Since it is not impossible that Wheeler's interpretation, on the other hand, finds its way into standard works on this side of the Atlantic, where *E. Chamaesyce* is unknown and *E. prostrata* not very well known, the net result of the shift in the concepts will be the creation of a double standard of nomenclature, the Old World understanding something and the New World something else whenever these two binomials happen to be used. In addition, the most knotty problems of nomenclature will have to be tackled and solved to everybody's satisfaction to decide what is to be proper name for the plant formerly known as *E. Chamaesyce*, and correctly to place its numerous trinomials. Looked at from every angle, an alteration of the classical application of *E. Chamaesyce* and *E. prostrata* can lead only to years of strife, disorder and confusion. It is clear, consequently that practical considerations of the most forceful nature forbid this alteration.

However, given certain conditions changes in existing names must be made. These conditions are satisfied, unquestionably, when current names conflict with the *International Rules of Botanical Nomenclature*. Not so long ago this writer has been forced to reinstate a practically unknown binomial, *E. Mili* Ch.-des-Moul. (Jour. Arnold Arb. **21**: 506. 1940), this taking the place of the ubiquitous and universally known *E. splendens* Boj. ex Hooker. The issue, then, must be faced whether the *Rules* actually forbid maintenance of the traditional concepts of *E. Chamaesyce* and *E. prostrata*. If they do, these two binomials must go, regardless of the practical consequences entailed in their rejection.

It is customary among sound taxonomists not to disturb existing nomenclature so long as changes can be avoided. It is customary, likewise, to honor the decisions of earlier authors whenever these decisions cannot be shown to be absolutely untenable. Convenience is best served by a steady nomencla-

ture and by the assurance that one author begins his work where another lays it down. Custom and convenience in this respect are sanctioned and upheld by the *Rules*. The *Rules* unequivocally state that fixity of nomenclature is their essential purpose [Art. 4(1), Amsterdam Rules, 1935], that names and forms must be rejected which throw taxonomy into confusion [Art. 4(2)], that existing names cannot be altered unless condemned by the *Rules* and shown to be manifestly untenable (Art. 17). A violation of these dicta, as is well known (Art. 2), entails illegitimacy, and cannot become the source of acceptable nomenclature. The *Rules* go so far as to give the right to an author to choose as valid either one of two or more binomials contemporaneously published (Art. 56), binding later authors to follow him. Likewise, the *Rules* admit that a straight misapplication can be maintained if it involves a generic name long in use, witness the maintenance of *Podocarpus* in the misapplied sense of Richard,<sup>2</sup> and of *Alpinia* Roxb. non L., *Protca* R. Br. non L. and *Banksia* L. f. non Forst., as Rehder (in Kew Bull. 344. 1935) has very pertinently pointed out.

The proponents of the old American Codes were much concerned with the proper choice of types and attempted to regulate it. Their conclusions, however, failed to win the approval of the International Congresses and were not received in the current *Rules*, which, if with some reserve, is a matter for gratification. The critical elaboration of nomenclatural tangles and controversial typifications often gives rise to questions that are incredibly involved, and it is but fair that a well-informed monographer or student should be allowed to select a type which best suits the needs of the case. Such selection, naturally, cannot conflict with the essential tenets of the *Rules*. Article 18 of the current *Rules* merely states that a specimen, description, or figure can serve as a type, it being otherwise well understood that no specimen, description, or figure shall be chosen which, without absolute need, subverts existing nomenclature and throws taxonomy into confusion.

With reference to sound usage and to the dicta of the *Rules*, therefore, it may be affirmed in the strongest terms that no author is bound to choose as the type of the name an entity (specimen, description, or figure) which leads him to violate the *Rules* by needlessly disturbing nomenclature. Nothing in the *Rules* enthrones a specimen in a position of privilege and power such as to wreck nomenclature. The type is not a pure abstraction but a means to an end. That type is to be chosen in every case which, be it specimen, description, or figure, protects stability of nomenclature and sanctions long usage.

Any author familiar with the species of *Euphorbia* of Linnaeus knows that in general these concepts are tainted with confusion and marred often-

<sup>2</sup> See for a discussion Pilger in Engl. Pflanzenr. 4<sup>5</sup>: 54 footn. 1903. This discussion fails to cover all the details of the case, but Pilger's proposals were accepted by the Congress of Vienna in 1905.



times by inept compilation. It is certainly convenient to abide by the Linnaean specimens whenever these specimens materially help in establishing the application of the Linnaean binomial, but it would be idle to speak of the Linnaean specimens as "types" in the modern sense. To dispose of a Linnaean species of *Euphorbia* it is necessary to take into account the current application of the name, its synonyms, its historical background and its specimens. All these elements must carefully be blended within a critical and broad approach.

*Euphorbia Chamaesyce* of the Linnaean synonyms and herbarium is a mixture of several entities which, in theory, it should be possible to reject as a *nomen confusum*. This mixture, however, has been in use for almost two centuries in a certain definite sense, and it is just as unwise to reject it as it is to alter its meaning. Not only the name must be saved, if at all possible, but its current application as well.

To a greater extent than the *Species Plantarum* (1753), the *Hortus Cliffortianus* (1737) actually reveals the taxonomic stuff of which the Linnaean thought is made. In the *Hortus Cliffortianus*, p. 198, Linnaeus treats the *Euphorbia* No. 12 (later to become *E. Chamaesyce*), as constituted of two entities. The first, which is the typic form, is referred to synonyms of Morison, Tournefort, Boerhaave, Caesalpinus, Bauhin, Clusius, Dalechampius, and Dodoens, which invariably apply to the plant known as *E. Chamaesyce* to traditional taxonomy. Only one synonym involves another entity, Sloane's "Chamaesyce" (Cat. Pl. Jam. 83. 1696) from Jamaica, of which Sloane tells us: "In locis aridioribus arenosis circa urbem *St. Jago de la Vega* nihil frequentius reperitur." This entity Fawcett & Rendle identify (Fl. Jam. 4: 342. 1920) as *E. thymifolia* L., a binomial which is as yet of very uncertain application. The variety is based on synonyms of Tournefort, Boerhaave, Morison, and Burman: it is evidently a pubescent entity, and in the main the same, it seems, as that which has been treated most commonly as *E. Chamaesyce* var. *canescens*. Linnaeus gives the following distribution: "*Crescit in agris & vineis aridis & arenosis Siciliae, Italiae, Galliae Narbonensis & Jamaicae . . .*," adding: "*Folia in Europaea magis orbiculata, in Americana oblonga & saepius macula fusca medio notata.*" Evidently, Linnaeus had a none too clear concept of the limits of this entity nor of its variety, and had seen European together with American material. Whether he correctly understood Sloane's plant is doubtful; Sloane himself had given for his "Chamaesyce" the usual references that apply to the weed of Europe, and on this ground Linnaeus had reason to admit it in his synonymy. It is clear at any rate that Linnaeus based his concept almost wholly on the plant of Europe, including American and Asiatic material under a mistaken assumption of range.

In the *Species Plantarum*, p. 455, the treatment is even less satisfactory.

No variety is admitted, the so-called *Dissertatio Euphorbiarum* is cited for the diagnostic phrase, as usual, and only synonyms of Linnaeus himself ("Hort. cliff. 198"), of Van Royen, Gmelin, Bauhin, and Clusius are introduced. The range this time is restricted to the Old World: "*Habitat in Europa australi, Sibiria.*" The Siberian entity is apparently *E. humifusa* Willd., or forms in its immediate vicinity. The bulk of the synonymy, however, both direct and implied, again applies to the European plant, the references to Bauhin and Clusius being maintained throughout between 1737 and 1753.

It will be seen that not a single one of the Linnaean references has anything to do with the works of Browne, this for the very simple reason that these works had not as yet come out of the press. It is strange, to say the least, that a specimen of Browne should be the "type" of *E. Chamaesyce* under these circumstances. Does the Linnaean diagnosis and range conform with the Browne collection which allegedly typifies the name? Not unequivocally so far as this writer can see.

A work of great relevancy, but almost invariably overlooked, is Crantz's *Institutiones Rei Herbariae*, published in 1766, only thirteen years after the release from the press of Linnaeus's *Species*. Crantz usually makes the Linnaean diagnoses his own with few changes, and refers them to one or two synonyms only, which are often critically chosen. Of *E. Chamaesyce* L. Crantz says (op. cit. 2: 457): "*Euphorbia dichotoma, foliis crenulatis subrotundis glabris, floribus solitariis axillaribus, caulibus procumbentibus.*" which with the single addition of "glabris" repeats the characterization of the *Species Plantarum* of Linnaeus. This addition is significant. Only one synonym is listed by Crantz, "*Chamaesyce. Clus. II. p. 187.*" This synonym appears both in the *Hortus Cliffortianus* and in the *Species Plantarum*.

Crantz's interpretation of *E. Chamaesyce* is quite acceptable under the current rules of nomenclature, for it basically agrees with the Linnaean concept of the species on the whole, with its characters and its synonyms. It has therefore the unequivocal status of a *descriptio emendata* effecting a clean-cut typification of the binomial. This amended description and this typification effected in 1766 and true to the traditional concept of the species between 1753 and 1941 cannot be lightly overthrown in 1941 to refer to a specimen of Browne, when Linnaeus does not cite the works of Browne and maintains, both in the *Hortus Cliffortianus* and in the *Species*, that *E. Chamaesyce* is a species of Southern Europe, at least *pro maxima parte*.

Clusius's characterization of "*Chamaesyce*" is definite, for he illustrates the plant and says (Rar. PL Hist. 6: clxxxvii, f. 1601): "*Copiosa ubiq; agro Salmanticensi, squallidis & petrosis locis, atque etiam inter ipsa vineta (quemadmodum & circa Monspelium) & plerisque alijs Hispaniae locis.*" This is *E. Chamaesyce* of the traditional concept, which grows in the stony

and waste grounds and in the vineyards of Salamanca in Spain, and Montpellier in Southern France. Clusius even gives the vernacular name current in Salamanca, "Noguerauela," explaining that this alludes to the shape of the seed.

In conclusion: *E. Chamaesyce* was rigorously interpreted and fully typified by Crantz in 1766, and this typification, knowingly or otherwise, has been used by thousands of authors throughout almost two centuries. Neither the *Rules* nor accepted usage make it necessary to reject Crantz's conclusions, belatedly taking up as the "type" of *E. Chamaesyce* a specimen which, chosen in the name of a hollow technicality, only serves to inflict untold damage upon classification. To use this specimen for subversive and confusing ends is a direct violation of Art. 4 and Art. 17 of the *Rules*, which plainly means that this use is illegitimate.

A fitting type of *E. Chamaesyce* is the reference to Clusius, a reference constantly upheld by Linnaeus and made by Crantz the base of a formal interpretation which has in its favor, everything else set aside, two centuries of constant usage. The application of *E. prostrata* may still be discussed. Nothing in the original publication rules out the plant so understood, but anyone who so wishes may claim that Aiton's binomial is a *nomen dubium* or a *nomen ambiguum*, and reinstate *E. callitrichoides* H.B.K. Conservative taxonomists will accept Boissier's interpretation [in DC. Prodr. 15(2): 47. 1862; Ic. Euph. 12. pl. 17. 1866], no doubt, understanding that this interpretation validly amends and certifies Aiton's original obscure diagnosis. It will be time to change the existing usage, when and if a specimen of Aiton is found having a clear holotypic status for *E. prostrata*, this specimen proving that Boissier errs. So long as this specimen is not forthcoming, at least the presumption stands that Boissier is right.

As a formal, final conclusion the following synonymy is here affirmed: *Euphorbia prostrata* Ait. Hort. Kew. 2: 139. 1789; cert. & emend. Boiss. in DC. Prodr. 15(2): 47. 1862, Ic. Euph. 12. pl. 17. 1866; auct. univ. Syn.: *E. Chamaesyce sensu* Wheel. Rhodora 43: 265. 1941; Contr. Gray Herb. 136: 265. 1941; non L. Sp. Pl. 455. 1753, cert. & emend. Crantz Inst. Rei Herb. 2: 457. 1766; Boiss. in DC. Prodr. 15(2): 34. 1862.

*Euphorbia Chamaesyce* L. in its correct traditional application is to be excluded from our flora. It may appear among us as a ballast plant, but this writer so far has not seen it.

#### THE ARNOLD ARBORETUM

#### JAMAICA PLAIN, MASSACHUSETTS

NOTE: While this article was in press, a study appeared (Darwiniana 6: 179-191. 1943) in which this writer dealt with the typification of *Euphorbia portulacoides* L. In that study clean-cut opinions were expressed (see op. cit. 183, and l.c. footnote, in particular) in unison with the ones voiced here. Unfortunately, in the "English Summary"

personally contributed by this writer a vital "not" was omitted on account of a typographic error, which this writer had no chance to correct. The summary in question recites in part (p. 190), "The author points out that the current International Rules of Nomenclature do bind a taxonomist to select as the type of a species a specimen rather than a description or figure." The awkwardness of this statement is evident on purely grammatical grounds. It reads as originally conceived and submitted to the editors, "The author points out that the current International Rules of Nomenclature do NOT bind a taxonomist to select as the type of a species a specimen rather than a description or figure." It is a matter of regret that the otherwise faithful Spanish summary, having been made directly from the English, reiterates the same error. It ought to read, "El autor sostiene que las Reglas . . . NO obligan . . ."

THE GENUS *CNIDOSCOLUS* IN MEXICO: NEW SPECIES  
AND CRITICAL NOTES\*

CYRUS LONGWORTH LUNDELL

In carrying out investigations for the Rubber Development Corporation of the United States Government in Mexico in 1943 to determine the sources of chicle gum, collections of *Cnidoscolus* were made in eleven states. The areas in which material was gathered range from seashore, arid and wet lowlands, through wet temperate uplands, to desert and mountainous regions of the high plateau.

Although the genus is of considerable economic importance and abundantly represented throughout Mexico, it has received very little attention from botanical collectors. Considering the investiture of stinging hairs on the plants, those of *C. elasticus* causing persistent sores, this is readily understood. Further, the fleshy nature of the thick twigs demands artificial heating to dry satisfactory specimens. Staminate and pistillate flowers as well as mature seeds are essential for the interpretation of the species, and only by making several trips to each area during the season can such material be obtained. Most of the material in herbaria is grossly inadequate.

In this preliminary study, twelve new species are proposed, all apparently referable to the Section *Calyptrerosolen* as delimited by McVaugh (1944). Along with field notes and other observations on various species, the transfer of *Jatropha Jurgensenii* Brig. and *J. Liebmannii* Muell. Arg. is made to the genus *Cnidoscolus*.

*CNIDOSCOLUS ACONITIFOLIUS* (Mill.) I. M. Johnston. Contr. Gray Herb. 68: 86. 1923. *Jatropha aconitifolia* Mill. Gard. Dict. ed. 8. *Jatropha* No. 6. 1768.

MEXICO: VERA CRUZ, east of Córdoba, along roadside at base of cliff, October 5, 1943, C. L. Lundell & Amelia A. Lundell 12530, 12530A, shrub, 6 ft. high, pith with transverse plates, latex white, calyx greenish outside, white within.

This collection agrees closely with the description of the species by Pax (1910). However, the staminate calyx is minutely puberulent rather than glabrous, and the ovary is only sparsely pubescent at base.

In the interpretation of *C. aconitifolius* by McVaugh (1943), the outer stamens are described as 4-5 mm. long. In Lundell & Lundell 12530, the outer stamens do not exceed 3 mm. including the fused basal part (1 mm.) of filaments. The staminate and pistillate flowers are slightly less than 1 cm. in length. The seeds from Lundell & Lundell 12530A agree in detail with the illustration by McVaugh (1943, fig. 12) based upon Rose & Rose 11474.

*C. tenuilobus*, described from the Pacific lowlands, approaches *C. aconitifolius*, as herein interpreted, and represents a geographical segregate. The

\* Publication of this paper is at the expense of the author.

androecium of both species is very similar, differing only in the smaller size of the gland in *C. aconitifolius*. In both species the staminate calyx lobes are shorter than the tube.

**Cnidoscolus albidus** Lundell, sp. nov. Frutex, 1 m. altus, pilosus et dense stimulosus. Folia longe petiolata, petiolo ad 15 cm. longo; lamina late cordata, 7.5–17 cm. longa, 9.5–21 cm. lata, supra pilosa, subtus albido-tomentosa, lobis 5, grosse lobulato-dentatis. Flores foeminei 9–11 mm. longi. Calyx utrinque sexus ad medium 5-lobus. Antherae biverticillatae. Ovarium pubescens.

Shrub, 1 m. high; twigs thick, densely pilose, the stinging hairs abundant, up to 5 mm. long; pith drying with transverse walls. Petioles rather stout, costate, up to 15 cm. long, densely pilose, the stinging hairs abundant; gland at apex of petiole large, fleshy, horseshoe-shaped. Leaf-blades broadly cordate, 7.5–17 cm. long, 9.5–21 cm. wide, with 5 primary lobes and veins, openly but narrowly cordate at base, upper surface dark green, densely pilose, bearing scattered stinging hairs along the primary and secondary veins, under surface white-tomentose, the stinging hairs few; the primary lobes extending below the middle of the blade, each conspicuously lobed and coarsely dentate, the secondary lobes and teeth spinescent. Inflorescence 6–15 cm. across; the peduncle 16–27 cm. long, densely pilose, the stinging hairs abundant; the primary branches of the inflorescence 2–6, forked 2–4 times, up to 5.5 cm. long, ascending, densely pilose and conspicuously armed with abundant stinging hairs, the ultimate branchlets bearing staminate flowers. Staminate flowers white; calyx finely tomentose, 15–17 mm. long, the tube slender, contracted at base into a short stipe, expanded above, obscurely costate, lobed to the middle, the lobes elliptic, spreading; staminal column pubescent at base, the stamens exserted; stamens 10 in two whorls; anthers 1.5–2 mm. long, equaling or slightly longer than the free part of filaments; staminodia 3, filiform, erect. Pistillate flowers solitary; calyx finely tomentose, deciduous in one piece, 9–11 mm. long, the tube cylindrical, the lobes oblong-elliptic, armed with a few stinging hairs; ovary finely tomentose; styles 3, dichotomously forked. Immature capsule ellipsoid, tomentose with fine short hairs, not beset with stinging hairs.

MEXICO: HIDALGO, above Jacala, off highway at kilometer 270, in scrub, August 19, 1943, *C. L. Lundell & Amelia A. Lundell 12394* (TYPE in the herbarium of Southern Methodist University).

Since the pistillate calyx is tubular at the base and deciduous as a whole, *C. albidus* is technically near *C. tubulosus* (Muell. Arg.) I. M. Johnst. As usually interpreted, *C. tubulosus* has been a nebulous entity to which most species with pistillate calyx tubular at base have been referred. Since type material is not available for examination, I am uncertain as to the application of the name. Pax (1910) described the staminate calyx of *C. tubulosus* as follows: "Calyx ♂ aperiens pyriformis, 5 mm. longus, deinde 6–8 mm. attingens, extus tomentellus." *C. elasticus*, *C. tepiquensis*, *C. spinosus*, and *C. albidus*, referable to this complex, all have the staminate calyx at least twice as large, and differ broadly in various other significant characteristics.

*C. albidus* is scarcely to be confused with any other Mexican species. Like *C. armatus*, it is a desert shrub of the high plateau.

**Cnidoscolus armatus** Lundell, sp. nov. Frutex, ad 1.5 m. altus, armatus. Folia petiolata, petiolo ad 8 cm. longo; lamina parva, rigide chartacea, ad

10.5 cm. longa, 11 cm. lata, ad basim villosa, glabrata, lobis 3 vel 5, lobulatis, remote dentatis. Inflorescentiae 3–7 cm. latae. Capsula ca. 11 mm. longa, glabrata, stimulosa. Caruncula 3–3.6 mm. lata.

Shrub, up to 1.5 m. high, the branches viciously armed with persistent rigid stinging hairs up to 1.3 cm. long; twigs stout, reddish, villous at the tips, conspicuously armed; pith with transverse plates. Petioles stout, costate, up to 8 cm. long, brown-villous along the lower side and at apex and base, the stinging hairs few; gland at apex of petiole small and fleshy, or absent. Leaf-blades small, drying stiff and chartaceous, up to 10.5 cm. long (from apex of petiole), up to 11 cm. wide, the basal sinus narrow, the primary lobes and veins 3 or 5, brown-villous at base, essentially glabrous otherwise, the stinging hairs few on both surfaces, appressed along the margin; the lobes extending at least three-fourths to base, narrowed below, the apical largest, the basal reduced and spreading, the apical and lateral usually with a prominent secondary lobe on each side at or above the middle, the margin remotely dentate with sharp teeth, the teeth gland-tipped. Inflorescence (in fruit) small, 3–7 cm. across, the peduncle stout, up to 10 cm. long, short villous-tomentose at first, glabrate, beset with stinging hairs; the primary branches 2 or 3, forked, with indument like that of peduncle. Staminate and pistillate flowers not seen. Capsules oval, about 11 mm. long (almost mature), glabrate, beset with slender stinging hairs. Seeds gray, not mottled, or with a few minute black spots chiefly along the margin, oblong-ellipsoid, somewhat flattened, about 9 mm. long (including the protruding caruncle), 5 mm. wide, slightly emarginate at base, acutish at apex; caruncle large, fleshy, protruding beyond apex of seed, 3–3.6 mm. wide, 1.6–1.9 mm. high, subtruncate and lobed at base, extending below the hilum, the fleshy lobes forming a cavity above the depressed hilum.

MEXICO: PUEBLA, off Tehuacán-Córdoba road, on dry hills east of Garcí-Crespo, in desert scrub, October 5, 1943, *C. L. Lundell & Amelia A. Lundell* 12525 (TYPE in the herbarium of Southern Methodist University).

In the absence of flowers, the relationship cannot be established; however, the leaf form is suggestive of *C. acronitifolius*. The species is exceptionally well-marked by the abundant long rigid stinging hairs persistent on the branches, by the gland-tipped hairs of the leaf margin, by the small seeds with protruding fleshy caruncle forming a cavity around the hilum, and by the small thick leaf blades. The villous indument usually is reddish. When present, the petiolar gland is small and fleshy.

Growing in the arid Tehuacán plateau region, the species appears to be isolated geographically.

**Cnidoscolus Chaya** Lundell, sp. nov. Frutex, ca. 3 m. altus, stimulosus, ceterum glaber. Folia petiolata, petiolo 12–15 cm. longo; lamina ad 15 cm. longa, 23 cm. lata, stimulosa, lobis 7, subpinnatifidis. Sepala ♂ 12 mm. longa, ad medium connata, puberula, alba. Stamina 10, biverticillata, 11 mm. longa. Capsula ca. 1 cm. longa, parce stimulosa. Caruncula ca. 1.5 mm. lata.

Arborescent shrub, scarcely 3 m. high; twigs thick, armed with scattered spine-like stinging hairs up to 4 mm. long, glabrous otherwise. Petioles stout, 12–15 cm. long, armed with short scattered stinging hairs, rather sparsely hirtellous at apex and base, otherwise glabrous, costate when dry; glands at apex of petiole suborbicular, fleshy, paired, one above the other. Leaf-blades broader than long, up to 15 cm. long (from apex of petiole), 23 cm. wide,

with deep broad basal sinus, the primary lobes and veins usually 7, with scattered short stinging hairs along the principal veins on both surfaces, pubescent at base, otherwise glabrous; lobed to within 2-3 cm. of base of blade, the lobes pinnatifid, cut at least halfway to their midribs into oblong or triangular secondary lobes as much as 6 cm. long, the apex of lobes and teeth of margin usually triangular, acute, ciliate with short appressed setae. Inflorescence small in flower, about 6 cm. across, the peduncle stout, about 24 cm. long, conspicuously armed with short stinging hairs, hirtellous at apex and base, otherwise glabrous; the primary branches of inflorescence beset with short stinging hairs, pubescent at the nodes. Staminate flowers white; calyx finely puberulent, 12 mm. long, lobed to the middle, the lobes elliptic, the tube narrow, scarcely 2 mm. in diameter, expanded above, the lobes spreading; stamens 10, in two whorls, 11 mm. long, exserted, basal 2 mm. of staminal column pubescent; lower (outer) stamens with filaments fused for 6 mm., free part of filaments 1.5-2 mm. long; upper (inner) stamens with filaments fused for about 8 mm., free part of filaments about 3 mm. long; anthers 1.5 mm. long; staminodia 2 or 3, filiform, about 4 mm. long, the tips often recurved. Pistillate flowers solitary in the forks of the branches; calyx deciduous, not seen. Young capsules glabrous, beset with scattered short stinging hairs. Capsules about 1 cm. long, beset with scattered stinging hairs. Seeds small, ellipsoid, 7 mm. long, 5 mm. wide, somewhat flattened; caruncle about 1.5 mm. wide, shriveled, subcordate at base above the small protruding hilum.

MEXICO: YUCATÁN, kilometer 27, Mérida-Progreso road, abundant in cactus thicket, July 30, 1938, *C. L. Lundell & Amelia A. Lundell* 8201 (TYPE in the herbarium of Southern Methodist University); vernacular names, *rtsaq*, *chaya*.

Like *C. Chayamansa*, this species appears to be allied to *C. aconitifolius*. In its paired petiolar glands it resembles *C. Chayamansa*, but differs notably from that species in the distinctive characteristics of the androeceum, abundance of stinging hairs, larger staminate flowers, and spreading primary veins of leaf.

CNIDOSCOLUS CHAYAMANSA McVaugh, Bull. Torrey Club 71: 466. 1944.

BRITISH HONDURAS: Orange Walk District, Honey Camp, cultivated in the dooryard, September 17, 1929, *C. L. Lundell* 494 (TYPE in the United States National Herbarium), a shrub 4 ft. high.

The plant, also known from Yucatan, apparently has not been found in the wild. A closely related native species is *C. Chaya*, described from Yucatan.

CNIDOSCOLUS ELASTICUS Lundell, Field & Lab. 12: 33. 1944.

MEXICO: SINALOA, near Chele, Arroyo de la Fresa, Rancho del Pino, altitude 2800 ft., May 9, 1943, *C. L. Lundell* 13021 (TYPE in the herbarium of Southern Methodist University), tree, 3 in. diameter, 22 ft. high, bark reddish, flowers white; same locality and date, *Lundell* 13020, tree, 6 in. diameter, 28 ft. high, bark papery and red, flowers white, gland at base of ovary orange; same locality, October, 1943, *C. L. Lundell & Rodolfo Gomez* 12613, tree, 6 in. diameter, 15 ft. high, capsules fleshy, ellipsoid, rostrate; road from Rancho del Pino to Copala, May 28, 1943, *C. L. Lundell & Manuel Itie* 12175, small tree, flowers white. DURANGO, Corral de Piedra, above Tayoltita, Piaxtla River, altitude 5000 ft., April 10, 1943, *Lundell* 13001, tree, 12 in.



diameter, 30 ft. high, bark thin, papery and reddish, staminate flowers white and fragrant; La Joya Mountain (or La Cruz Larga), above Corral de Piedra, Piaxtla River, altitude 5000 ft., April 11, 1943, *Lundell 13008*, tree, 6 in. diameter, 15 ft. high, flowers white; Ojito (or Encinal), above Corral de Piedra, Piaxtla River, altitude 5000 ft., April 12, 1943, *Lundell 13009*, tree, 4 in. diameter, 12 ft. high, flowers white, latex white; Ejido Campanilla, San Felipe de las Minas, near Huajupa, San Lorenzo River watershed, on mountain side, altitude about 5200 ft., April 27, 1943, *Lundell 13012*, tree, 6 in. diameter, flowers white; same locality and date, *Lundell 13013*, small tree, flowers white; below Otaes, on trail to Huajupa, April 26, 1943, *Lundell 13080*, seeds collected in that vicinity by Indians during the previous season; Rancho de la Mina, west of Los Remedios, April 15, 1943, *H. S. Gentry 6820*, reddish barked tree, 18 to 21 ft. high, with blunt twigs, leafless. TEXAS: Dallas County, Agricultural Research Station, near Renner, September 9, 1944, *Lundell 13302*, seedlings six months old grown from seeds obtained in Durango, Mexico.

On March 17, 1944, seeds of *C. elasticus*, obtained at Otaes in the interior mountains of Durango, were planted at the Agricultural Research Station of the Institute of Technology and Plant Industry. In the test plot, the germination of seeds planted in the field was approximately 90 per cent. After a slow start, the seedlings began to grow rapidly in August and September. In September three of the plants flowered. By the middle of November, 1944, at an age of eight months, the seedlings had reached a maximum height of six feet and a diameter up to two inches at the base, a remarkable rate of growth.

The heavy frost of November 27, 1944, at Dallas, when the temperature dropped to 29° F, killed the leaves and tender growth. On the same date there was considerable damage to the cortex for latex oozed out over the stem to coagulate into small scattered lumps. Subsequent temperatures as low as 20° F killed all of the stem except the woody base. Although the roots and base survived a temperature of 20° F, the critical temperature for the species is about 30° F, and no commercial plantings should be made where heavy frosts occur.

The plantation possibilities of *C. elasticus* are the subject of current investigations. The gum from the tree is considered by the chewing gum industry to be a satisfactory substitute for jelutong, formerly imported from the Far East. Intensive exploitation of the wild stand in Durango and Sinaloa is underway.

*C. elasticus* and the closely related *C. tepiquensis*, the two rubber-yielding species, both have solid pith. In all other members of the Section *Calyptrosolen*, the pith has transverse plates when dry. These differences are of possible subsectional importance.

**Cnidoscolus Hernandezii** Lundell, sp. nov. Frutex, pilosus et dense stimulosus. Folia petiolata, petiolo ad 16 cm. longo, eglanduloso; lamina ad

13.5 cm. longa, 18 cm. lata, cordata, pilosa, lobis 5, remote dentatis. Inflorescentiae ad 14 cm. latae, pilosae et stimulosae. Capsula ca. 1.2 cm. longa, glabra. Caruncula 2.5–2.8 mm. lata.

Shrub with thick branches; twigs very stout, armed with abundant amber colored stinging hairs up to 6 mm. long, pilose with short hairs; pith drying with transverse plates. Petioles stout, up to 16 cm. long, pilose, armed with scattered stinging hairs; eglandular at apex of petiole. Leaf-blades broader than long, up to 13.5 cm. long, 18 cm. wide, the basal sinus deep, narrow, rounded, the primary lobes and veins usually 5, pilose on both surfaces, the hairs dense along the principal veins, with scattered stinging hairs on upper surface and along margin; the primary lobes extending to middle of blade, oblong-elliptic or obovate-elliptic, the margin of lobes rather remotely dentate with acuminate teeth 2–10 mm. long, the teeth on margin of apical 3 lobes minute below, large above the middle. Inflorescence (in fruit) rather large, up to 14 cm. wide, the peduncle rather slender, up to 23.5 cm. long, densely pilose and conspicuously armed with stinging hairs; the primary branches of the inflorescence usually 2 or 3, forked, covered with indument like that of peduncle. Staminate and pistillate flowers not seen. Ovary pubescent at apex and base, otherwise glabrous; style pubescent. Capsule oval, depressed at apex, about 1.2 cm. long, glabrous. Seeds oblong-ellipsoid, somewhat flattened, 8.5–9 mm. long, about 5.5 mm. wide, mottled at maturity primarily along margin, acutish at apex; caruncle fleshy, yellowish, 2.5–2.8 mm. wide, subtruncate or rounded, with two small fleshy lobes at base on each side of the small hilum, crested medianally above the hilum.

MEXICO: OAXACA, Santa María del Tule, October 17, 1943, *Efraim Hernandez X. s. n.* (TYPE in the herbarium of Southern Methodist University); vernacular name, *mala mujer*.

*C. Hernandezii* is anomalous in that the petioles are eglandular at apex. The pilose twigs, leaves and inflorescences, abundant short amber colored stinging hairs, essentially glabrous ovary, and distinctive small seeds with crested caruncle bilobulate at the subtruncate base are distinguishing characteristics. In the absence of flowers, its affinities are uncertain.

**Cnidoscolus Jurgensenii** (Briq.) Lundell, comb. nov. *Jatropha Jurgensenii* Briq. Ann. Cons. Jard. Bot. Genève 4: 229. 1900.

**Cnidoscolus Liebmannii** (Muell. Arg.) Lundell, comb. nov. *Jatropha Liebmannii* Muell. Arg. Linnaea 34: 212. 1865.

No specimens have been seen which may be referred to this species, and a study of the type is essential to definitely determine its status. As described, the laciniate lobes of the leaves, the glabrous staminal tube, combined with a pistillate calyx tubular to the middle indicate that a distinct species is represented.

**Cnidoscolus macrandrus** Lundell, sp. nov. Frutex, parce stimulosus. Folia petiolata, petiolo ad 13 cm. longo; lamina membranacea, ad 15 cm. longa, 22 cm. lata, cordata, parce stimulosa, glabrata, lobis 5 vel 7, cuspidato-acuminatis, remote dentatis. Inflorescentiae parvae, ad 8 cm. longae. Sepala ♂ 15–16 mm. longa, ad medium connata. Stamina 10, biverticillata, 8 mm. longa. Antherae 3 mm. longae, 2 mm. latae.

Shrub; twigs stout, with a few short stinging hairs at apex only, sparsely pubescent at the nodes, glabrate; pith with transverse plates. Petioles cos-

tate, up to 13 cm. long, sparsely pubescent at first with subappressed hairs, glabrate, unarmed or beset with few short stinging hairs; gland at apex of petiole fleshy, slightly elevated. Leaf-blades very thin, broader than long, up to 15 cm. long (from apex of petiole), up to 22 cm. wide, the basal sinus open and rounded, the primary lobes and veins 5 or 7, with scattered small stinging hairs on upper surface and along margin at first, pubescent at base on both surfaces, glabrate, the margin ciliate with appressed hairs, otherwise glabrous; lobed at least three-fourths to base of blade, the lobes oblanceolate, cuspidate-acuminate, the margin of lobes dentate with small acute and larger acuminate teeth, without conspicuous secondary lobes. Inflorescence small, up to 8 cm. long, 4-5 cm. wide, the peduncle slender, up to 6 cm. long, sparsely pubescent, beset above middle with short stinging hairs; the primary branches of inflorescence 2 or 3, forked, pubescent and beset with scattered stinging hairs. Pistillate flowers and fruits not seen. Staminate flowers white; calyx sparsely pubescent, the buds obovate, the mature calyx 15-16 mm. long, short-stipitate at base, campanulate, the tube wide, lobed to the middle, the lobes up to 7 mm. long, 6 mm. wide, elliptic. Stamens 10, in two whorls, 8 mm. long, villous at base of staminal column; the gland lobed, thick; lower (outer) stamens with filaments fused 2-2.5 mm., free part of filaments about 3 mm. long; upper (inner) stamens with filaments fused for about 4 mm., free part of filaments about 3 mm. long; anthers 3 mm. long, 2 mm. wide; staminodia 3, filiform, about 4 mm. long.

MEXICO: VERA CRUZ, between Jesus Carranza and Suchilapan, altitude 200 ft., along edge of trail in wet lowland forest, January 24, 1943, *C. L. Gilly, Sr. 4713* (TYPE in the herbarium of Southern Methodist University).

The reduced inflorescence, small leaves, large staminate flowers, large anthers, and the peculiarities of the staminal column set this species apart.

*CNIDOSCOLUS MULTILOBUS* (Pax) I. M. Johnst. Contr. Gray Herb. **68**: 86. 1923. *Jatropha multiloba* Pax, Pflanzenreich IV. **147**: 107. 1910.

MEXICO: SAN LUIS POTOSÍ, El Banito, near Valles, July 14, 1943, *C. L. Lundell & Amelia A. Lundell 12244*, a shrub or tree, up to 6 in. diameter, 20 ft. high, latex white, calyx white; Tamazunchale, along rocky ravine off highway to Chapulhuacán, July 15, 1943, *Lundell & Lundell 12260*, low shrub, almost glabrous, viscid; same locality and date, *Lundell & Lundell 12261*, arborescent shrub, calyx white.

The type of *C. multilobus*, *Bourgeau 2231* from Orizaba, Vera Cruz, is not available, and no authentic specimens of the species have been seen. That collections representing a series of closely related species are now being pigeon-holed under this name appears probable.

The collections from San Luis Potosí are being referred to *C. multilobus* tentatively. The seeds of *Lundell & Lundell 12244* have the same caruncle as illustrated by McVaugh (1943, fig. 13). *Lundell & Lundell 12260* is anomalous in that the leaves are viscid when fresh, a condition not noted in any other collection. The leaf-blades of *Lundell & Lundell 12244* and *12261* are velutinous. In all three collections, the apex of the petiole bears two mammae-form fleshy glands.

Of the new species proposed, *C. macrandrus*, *C. parviflorus*, and *C. velutinus* belong to the *C. multilobus* complex.

*Cnidoscolus orbiculatus* Lundell, sp. nov. Herbacea, ad 1 m. alta, caulis dense stimulosus. Folia petiolata, petiolo 1.5-8.5 cm. longo, stimulosus, supra

villosa; lamina orbiculata, ad 9 cm. longa, 14.5 cm. lata, profunde cordata, stimulosa, supra parce villosa, subtus parce hispida, lobis 3, grosse sinuato-dentatis. Inflorescentiae foliis breviores, 1.5–3, raro ad 5 cm. longae, stimulosae. Sepala ♂ stimulosa, 12–13 mm. longa, ad medium connata. Stamina 10, biverticillata. Sepala ♀ 9–11 mm. longa, stimulosa. Capsula ca. 1.4 cm. longa, rostrata. Caruncula 3 mm. lata.

Perennial herb up to 1 m. high, bushy; stems stout, densely armed with slender stinging hairs up to 11 mm. long; twigs comparatively slender, densely covered with stinging hairs of various lengths, pubescent at the nodes, glabrous otherwise. Petioles rather slender, costate, 1.5–8.5 cm. long, beset with slender stinging hairs, short villous on upper surface, otherwise glabrous; gland at apex of petiole suborbicular, large, fleshy. Leaf-blades broader than long, orbicular in outline, up to 9 cm. long (from apex of petiole), up to 14.5 cm. wide, cordate with deep open basal sinus, the primary veins usually 7, shallowly 3-lobed at apex, beset with slender stinging hairs on both surfaces, short villous at base and along primary veins on upper surface, sparsely hispid over the entire lower surface; the margin appressed hispid, coarsely sinuate-dentate, the teeth up to 1.5 cm. long, broad at base, acuminate, spinescent but not hair-like at tips. Flowers in small cymes hidden at the ends of leafy branches; inflorescence usually 1.5–3 cm. long including peduncle, rarely up to 5 cm. long with mature fruits; the peduncle and branches short villous in a single line, beset with stinging hairs, Staminate flowers white; calyx lobes beset with stinging hairs, the calyx otherwise entirely glabrous, 12–13 mm. long, the tube slender at base, gradually expanded upward, the lobes extending to the middle, elliptic; stamens 10, in two whorls, 9 mm. long, not stipitate above the gland, the basal 0.5 mm. of staminal column pubescent; lower (outer) stamens with filaments fused for 3.5 mm., free part of filaments about 1.5 mm. long, anthers about 1.5 mm. long; upper (inner) stamens with filaments fused for about 6 mm., free part of filaments about 2 mm. long, anthers about 1.5 mm. long; staminodia 1–3, about 2 mm. long, filiform. Pistillate flowers solitary in the forks of the branches; calyx 5-lobed to base, 9–11 mm. long, the lobes oblanceolate-linear, rounded at apex, beset above middle with stinging hairs, otherwise entirely glabrous. Ovary with a ring of hairs at base, otherwise glabrous, rostrate at apex, the base of style fused, styles 3, glabrous, forked. Capsules broadly oval, about 1.4 cm. long including abruptly narrowed rostrate apex, beset with scattered stinging hairs, pubescent at base, glabrous otherwise. Seeds mottled brown, oblong, 8 mm. long (including the protruding caruncle), 5 mm. wide, apex and base subtruncate; caruncle fleshy, 3 mm. wide, extending below the hilum, base broadly rounded, 2-lobed, the small hilum seated between the protruding lobes.

MEXICO: MORELOS, about 9 kilometers beyond Alpuyecá on Cacahuamilpa road, in fallow field and along roadside, July 31, 1943, *C. L. Lundell & Amelia A. Lundell 12312* (TYPE in the herbarium of Southern Methodist University).

*C. orbiculatus* has affinity to *C. calyculatus* (Pax & Hoffm.) I. M. Johnst., *C. angustidens* Torr., and *C. Pringlei* I. M. Johnst. These herbaceous species are very closely allied, and additional field work will be necessary to obtain adequate specimens for the delimitation of the entities. In many respects, *C. orbiculatus* agrees with the description of *C. calyculatus*, but differs at

once in having fused rather than free filaments in the lower (outer) staminal series, and longer calyces glabrous except for the stinging hairs. In *C. angustidens* the inflorescence is comparatively large, the teeth of the leaves are long and slender, the seeds are larger, and the leaves are conspicuously lobed. *C. Pringlei*, known only from description, has smaller more conspicuously lobed leaves, a laxly flowered inflorescence, puberulent calyces, and smaller capsules. Noteworthy in *C. orbiculatus* is the small congested inflorescence almost concealed by the leaves.

**Cnidoscolus parviflorus** Lundell, sp. nov. Frutex, 2 m. altus, parce stimulosus, glabratus. Folia longe petiolata, petiolo ad 21 cm. longo; lamina ad 18 cm. longa, 22 cm. lata, profunde cordata, pilosa, lobis 3 vel 5, supra dentatis. Sepala ♂ 6.5–9 mm. longa, ad medium connata. Stamina 10, raro 6 vel 9, biverticillata, ca. 6 mm. longa. Sepala ♀ 4–4.5 mm. longa. Ovarium pubescens. Capsula 12 mm. longa. Caruncula parva, ca. 1 mm. lata.

Shrub, 2 m. high, practically unarmed; twigs rather slender, beset with scattered ascending stinging hairs scarcely 2 mm. long, short pilose, glabrate with age; pith with transverse plates. Petioles densely short pilose, usually unarmed, up to 21 cm. long; glands at apex fleshy, entire or shallowly lobed, slightly elevated. Leaf-blades slightly broader than long, up to 18 cm. long (from apex of petiole), up to 22 cm. wide, deeply cordate at base, the sinus open and rounded, the primary lobes 3 or 5, pilose on both surfaces, the hairs thinner and shorter on upper side, beset with a few small subappressed stinging hairs along margin and primary veins, otherwise unarmed; lobed to below the middle of blade, the apical lobes obovate-oblong, acuminate, the sinuses open and rounded, the margin of lobes conspicuously dentate above the middle with few acute or acuminate teeth up to 1.2 cm. long. Inflorescence small and flat, up to 6.5 cm. wide, the peduncle up to 22 cm. long, the peduncle and branches densely pubescent with soft short somewhat matted hairs, unarmed or beset with very few small stinging hairs. Staminate flowers white; calyx finely tomentose, 6.5–9 mm. long, tube subcampanulate, lobed to the middle, the lobes elliptic or suborbicular, up to 4 mm. wide, cordate at base; stamens usually 10, sometimes reduced to 6 or 9, in two whorls, about 6 mm. long, basal 1 mm. of staminal column pubescent; the staminal column 2 mm. high; lower (outer) stamens with filaments free for about 2 mm.; upper (inner) stamens with filaments free for 3.5–4 mm.; the free part of both whorls attached to staminal column at same point; anthers about 1.5 mm. long; staminodia 1–3, filiform, up to 5.5 mm. long. Pistillate flowers solitary in the forks of the branches; calyx finely tomentose, lobed to the base, the lobes oblong, 4–4.5 mm. long; ovary densely pubescent with short hairs; styles sparsely pubescent, sessile. Capsules subglobose, about 12 mm. long, sparsely pubescent and beset with short stinging hairs, warty over the entire surface. Seeds brown, oblong-ellipsoid, slightly compressed, about 9 mm. long, 5.5 mm. wide; caruncle small, scarcely 1 mm. wide, narrowed to base above hilum, the margin curled.

MEXICO: SAN LUIS POTOSÍ, off Xilitla road, on mountain side above the Axtla River, August 21, 1943, *C. L. Lundell* & *Amelia A. Lundell* 12427 (TYPE in the herbarium of Southern Methodist University).

*C. parviflorus* is near *C. multilobus*, but the smaller flowers, smaller anthers, distinctive caruncle scarcely 1 mm. wide, persistently pubescent leaves, and the almost complete absence of stinging hairs distinguish it. The

short staminal column with free filaments of both whorls attached at the same point at apex is noteworthy. In some staminate flowers there are as few as six stamens, an aberrant condition not noted among other Mexican species.

**Cnidoscolus rostratus** Lundell, sp. nov. Frutex, 1–2 m. altus, stimulosus et dense pilosus. Folia longe petiolata, petiolo ad 14 cm. longo; lamina cordata, 8–17 cm. longa, 6.8–17 cm. lata, velutina, lobis 3, raro 5, dentatis. Inflorescentiae parvae, pilosae et parce stimulosae. Sepala ♂ ca. 13 mm. longa, ad medium connata. Stamina 10, biverticillata. Sepala ♀ linear-oblonga, ca. 9 mm. longa. Ovarium tomentosum, rostratum. Capsula rostrata.

Shrub, 1–2 m. high; branches thick, tuberculate, the tubercles covered with coarse stinging hairs; twigs stout, densely pilose and covered with coarse subappressed stinging hairs up to 7.5 mm. long; pith continuous, without dissepiments before drying. Petioles rather stout, up to 14 cm. long, densely pilose, the stinging hairs few and scattered; gland at apex of petiole large, fleshy, suborbicular to reniform. Leaf-blades cordate, 8–17 cm. long, 6.8–17 cm. wide, usually with 3, rarely 5 primary lobes and veins, the basal sinus open, subtruncate or rounded, both surfaces densely pilose (velutinous), the stinging hairs small, few and scattered on upper surface, often absent from lower surface; the primary lobes extending to the middle of the blade, the terminal one obovate, each acuminate and spinescent, the margin coarsely toothed with few acuminate spinescent teeth, these terminating the secondary veins. Inflorescence small, 3–4 cm. wide, the peduncle stout, up to 14 cm. long, densely short pilose and armed with scattered stinging hairs; the primary branches of the inflorescence usually 2 or 3, forked 1 or 2 times, densely short pilose and armed with scattered small stinging hairs. Staminate flowers white (only 1 lodged in inflorescence seen); calyx pubescent, about 13 mm. long, lobed to the middle, the lobes oblong-elliptic, spreading; staminal column stipitate above the annular gland, pubescent at base; lower stamens included, the filaments united into a tube only about 1.5 mm. long; stamens 10 in two whorls; anthers of lower (outer) ones subsessile, 2.2 mm. long; anthers of upper ones slightly smaller, exserted, the free part of filaments about 2.5 mm. long; staminodia 2, less than 1 mm. long. Pistillate flowers solitary in the forks of the branches; calyx pubescent, the lobes splitting almost to the base, about 9 mm. long, linear-oblong, beset with a few stinging hairs. Ovary tomentose, rostrate at apex, the thick base of style persistent. Immature capsules ovoid-ellipsoid, costate, conspicuously rostrate, pubescent, not armed with stinging hairs.

MEXICO: OAXACA, north of Huajuápam, on black arid limestone hills of high plateau, July 26, 1943, *C. L. Lundell* 12304 (TYPE in the herbarium of Southern Methodist University).

The pistillate calyx is lobed almost to the base as evidenced by the fragmentary flowers available. Although of doubtful relationship, the species is very distinct.

Among arborescent members of the genus in Mexico, only *C. elasticus* has a rostrate capsule similar to that of *C. rostratus*. Another peculiarity of the species is the presence on older wood of tubercles densely covered with stinging hairs.

CNIDOSCOLUS SOUZAE McVaugh, Bull. Torrey Club 71: 468. 1944.

MEXICO: CAMPECHE, Tuxpeña, in secondary growth, January 15, 1932, *C. L. Lundell* 1189 (TYPE in the Gray Herbarium), a shrub. YUCATAN, near

Piste, abundant in low thicket, June 14, 1938, *C. L. Lundell & Amelia A. Lundell 7549*, a shrub, 6–12 ft. high, flowers white.

The 1938 collection from Yucatan differs slightly in having staminate flowers up to 12 mm. long, but agrees rather closely in other characteristics, notably in having the filiform stipitate glands at the apex of the petiole and the gland-tipped setae of the leaf margin.

The stipitate petiolar glands of *C. Souzae* and the substipitate mammae-form glands in *Lundell & Lundell 12244* from San Luis Potosí, referred tentatively to *C. multilobus*, suggest a relationship. Further, the leaves of *C. Souzae* are similar in form to those of *C. multilobus* and allied species. There is considerable justification for the reference of this well-marked species to the Section *Calyptrosolen*.

**Cnidoscolus spinosus** Lundell, sp. nov. Arbor parva ad 5 m. alta; rami crassi, stimulosi, ceterum glabri. Folia longe petiolata, petiolo ad 22.5 cm. longo; lamina 9–20 cm. longa, 12–29 cm. lata, ad basim cordata, parce stimulosi, glabrata, lobis 3 vel 5, apice rotundatis, dentatis. Inflorescentiae ad 25 cm. latae, longe pedunculatae. Sepala ♂ puberula, ca. 13 mm. longa, ad medium connata. Stamina 10, biverticillata. Sepala ♀ ca. 8 mm. longa, ad medium connata. Capsula 1 cm. longa, stimulosa. Caruncula 2.5 mm. lata, basi cordata.

Arborescent shrub or small tree up to 5 m. high; pith with transverse plates; twigs thick, armed with rigid spine-like stinging hairs up to 1.3 cm. long, glabrous otherwise. Petioles thick, up to 22.5 cm. long, puberulent at apex and base, the stinging hairs few, scattered, glabrous otherwise, drying costate; gland at apex of petiole large, fleshy, suborbicular. Leaf-blades cordate or cordate-ovate, 9–20 cm. long, 12–29 cm. wide, with 3 or 5 primary lobes and veins, the basal sinus narrow and deep, upper surface covered at first with stinging hairs, these scattered and inconspicuous or absent at maturity, otherwise glabrous, undersurface puberulent along primary veins at base, otherwise glabrous, the stinging hairs persistent along margin of basal sinus; the primary lobes extending almost to middle of blade, the terminal and two lateral ones (in 5-lobed leaves) obovate-ovate, the margin of lobes dentate, the teeth triangular-acuminate, up to 1 cm. long. Inflorescence large, standing out above the leaves, up to 25 cm. across, the peduncle thick, up to 45 cm. long, puberulent at apex and base, armed with long stinging hairs, otherwise glabrous; the primary branches of the inflorescence usually 3 or 4, forked up to 6 times, armed with stinging hairs. Staminate flowers white; calyx finely puberulent, about 13 mm. long including a short basal stipe, lobed to the middle, the lobes elliptic, spreading; staminal column pubescent at base, short stipitate above gland; stamens 10, in two whorls; lower stamens included in tube, the united filaments about 2 mm. long, subequal, anthers about 2.3 mm. long; upper (inner) stamens exserted, the free part of filaments about 2.5 mm. long, the anthers 2 mm. long; staminodia 3, filiform, equaling the upper stamens, about 3.5 mm. long. Pistillate flowers solitary in the forks of the branches; calyx deciduous in one piece, finely pubescent, about 8 mm. long, 5-lobed to the middle or lower, the lobes elliptic. Ovary hirtellous at apex and base, otherwise glabrous; styles 3, hirtellous, forked 3 times, spreading. Capsules broadly ellipsoid, 1 cm. long (almost mature), armed with stinging hairs, otherwise glabrous. Immature seeds oblong-ellipsoid, 8.5 mm. long, 6 mm. wide, somewhat flattened; caruncle 2.5 mm. wide, flat, cordate at base.

MEXICO: JALISCO, Municipio Puerto Vallarta, Chimo, along seashore, altitude 6-30 ft., June 8, 1943, *C. L. Lundell 13028, 13029* (TYPE in the herbarium of Southern Methodist University); vernacular name, *hiedra*.

*C. spinosus* is abundant along the seashore at Chimo, growing where salt spray often covers the plants. It is evidently a local endemic easily recognized by the dense investiture of stiff stinging hairs, essentially glabrous leaves with rounded lobes, and exceptionally large inflorescences. The pistillate calyx, united at base and deciduous in one piece, is typical of the small complex of species which includes *C. tepiquensis* of the same region.

From tapping cuts in the cortex of *C. spinosus*, latex oozes out in quantity but does not flow sufficiently to permit collection.

***Cnidoscolus tenuilobus* Lundell, sp. nov.** Frutex, 1-2 m. altus, fere estimulosus. Folia petiolata, petiolo ad 21 cm. longo, parce setuloso; lamina ad 20 cm. longa, 30 cm. lata, ad basim cordata, adpresso-setulosa, lobis 5, pinnatifidis, acuminatis. Sepala ♂ puberula, 9-10.5 mm. longa. Stamina 10, 6.5-7.5 mm. longa, biverticillata. Sepala ♀ libera, ca. 7 mm. longa, puberula, stimulosa. Capsula ca. 8 mm. longa, stimulosa. Caruncula 3 mm. lata, basi cordata.

Slender shrub, 1-2 m. high; twigs densely puberulent, practically unarmed, the stinging hairs less than 2 mm. long; pith with transverse plates. Petioles slender, up to 21 cm. long, sparsely setulose with short recurved hairs, densely puberulent at base, glabrous otherwise; gland at apex of petiole fleshy, large, reniform. Leaf-blades broader than long, up to 20 cm. long (from apex of petiole), 30 cm. wide, with broad open round sinus at base, the primary lobes and veins usually 5, sometimes with 2 additional smaller lobes at base, setulose over the entire upper surface with short appressed hairs, setulose along the principal veins on undersurface, sparsely pubescent at base, the margin appressed-setulose, otherwise glabrous; lobes slender, 5-12 mm. wide, cut almost to the base of blade, pinnatifid, the secondary lobes slender, less than 15 mm. wide, the primary and secondary lobes with few triangular teeth up to 15 mm. long, the lobes and teeth acute or acuminate. Inflorescence comparatively small, up to 8 cm. across top, the peduncle slender but erect, up to 40 cm. long, puberulent, sparsely but persistently setulose; the primary branches of inflorescence 2 or 3, forked, densely puberulent and setulose. Staminate flowers with greenish calyx, minutely puberulent, 9-10.5 mm. long, the lobes 3-3.5 mm. long, broadly elliptic or ovate-elliptic, the tube large, about 2.5 mm. in diameter at base, gradually expanded above; stamens 10, in two whorls, 6.5-7.5 mm. long; the gland at base shallowly lobed, 1.5 mm. in diameter; lower (outer) stamens with filaments fused scarcely 1 mm. at base, free part of filaments 1.5-2 mm. long, the base of column densely villous for at least 1 mm.; upper (inner) stamens with filaments fused 4-5 mm., free part of filaments 1.5-2 mm. long; anthers up to 1.5 mm. long, the upper slightly smaller; staminodia 3, filiform, up to 4 mm. long. Pistillate flowers solitary in the forks of the branches, pedicellate; calyx 5-lobed to base, greenish, about 7 mm. long, the lobes finely puberulent, setulose with short stinging hairs, linear-oblong, 1.8-2.5 mm. wide; ovary sparsely appressed hairy at base, otherwise glabrous; styles 3, thick, spreading, glabrous, multi-lobed. Capsules subglobose-ellipsoid, about 8 mm. long, beset with short stinging hairs. Seeds gray, inconspicuously mottled with black, obovoid-ellipsoid, about 7 mm. long, 5 mm. wide, base



slightly emarginate, rounded, apex acutish; caruncle fleshy, up to 3 mm. wide, with thick rounded smooth edges, cordate at base, the broad basal lobes extending slightly below the small protruding hilum.

MEXICO: GUERRERO, near Acapulco, kilometer 417 along highway, on roadside ledges, October 20, 1943, *C. L. Lundell & Amelia A. Lundell 12583* (TYPE in the herbarium of Southern Methodist University).

From *C. aconitifolius*, which it approaches, *C. tenuilobus* is distinguished by narrowly lobed pinnatifid leaves, appressed setulose upper surface of the leaf blades, setulose calyx lobes of the pistillate flowers, gland at base of androecium 1.5 mm. in diameter (less than 1 mm. wide in *C. aconitifolius*), and by a flat cordate caruncle with rounded smooth edges.

CNIDOSCOLUS TEPIQUENSIS (Cost. & Gall.) McVaugh, Bull. Torrey Club **71**: 466. 1944. *Cnidoscolus tepiquensis* (Cost. & Gall.) Lundell, Field & Lab. **12**: 36. 1944. *Jatropha tepiquensis* Cost. & Gall. Rev. Gen. Bot. **18**: 391. 1906.

MEXICO: NAYARIT, Municipio San Blas, Ejido La Palma, June 14, 1943, *C. L. Lundell & Manuel Itie 12171*, tree, branches verticillate, flowers white; Municipio San Blas, Ejido Aticama, June 15, 1943, *Lundell & Itie 12172*, tree, flowers white; Acaponeta, Ejido San Jose de Gracia, September 21, 1943, *Efraim Hernandez X. s. n.*, tree in fruit. SINALOA, Hacienda Chele, Rancho del Pino, on mountain side, altitude 1500 ft., June, 1943, *Lundell & Itie 12171*, small tree, flowers white. JALISCO, Municipio Puerto Vallarta, on hills above Chimo, in coquital, June 9, 1943, *C. L. Lundell 13035*, tree, 3 in. diameter, 30 ft. high, branches verticillate in threes, bark white, pith solid and continuous in twigs, flowers white, latex white; same locality and date, *Lundell 13036*, tree, 8 in. diameter, 35 ft. high, branches verticillate in threes, pith solid and continuous, flowers white, latex white; Municipio Puerto Vallarta, Arroyo de las Amapas, June 20, 1943, *C. L. Lundell & Rodolfo Gomez s. n.*, flowers white.

*C. tepiquensis*, of importance as the source of lowland chilte gum, is perhaps the largest tree in the genus, reaching a measured size of 18 inches in diameter and 80 feet high. Trees up to 3 feet in diameter and 100 feet high have been reported from Jalisco. The species has been found as far north as Concordia, Sinaloa, and it ranges through Nayarit into northern Jalisco as far south as Tomatlan. The best stands are in Municipio Puerto Vallarta, Jalisco.

In southern Sinaloa no stands of commercial importance have been located; the trees are found there principally along banks of arroyos and creeks. In Nayarit, approximately 125,000 acres were surveyed in the districts of Ixcuintla, San Blas, and Compostela. In this region, 2 to 2.5 per cent of the area is covered with chilte stands averaging about 40 trees per acre. In the coastal area of Nayarit, the tree is an associate of the *coquito* palm, a species of *Orbignya*. Inland the clearing for agriculture has destroyed most of the virgin forest, so that the species is found chiefly in secondary growth.

In the Municipio Puerto Vallarta, Jalisco, where the *coquito* palm forest has been protected, chilte is one of the dominant elements of the vegetation.

On the seaward slopes of the mountains from Puerto Vallarta to Corrales, there is a continuous belt of the *coquito* palm and *C. tepiquensis*.

*C. tepiquensis* is the source of all the chilte gum from the Pacific lowlands. It is known as chilte, chilte blanco, and chicle. Although locally exploited over a period of years for use in the manufacture of novelties, commercial exploitation on a large scale did not get underway until 1942. The dry gum has an average rubber content of approximately 30 per cent.

In Sinaloa and Nayarit exploitation has been carried out on a very limited scale, and the stands in Nayarit are practically virgin. The principal source of lowland chilte has been the Municipio Puerto Vallarta in Jalisco; here a production up to 13 tons per week was reached during the 1942-1943 season.

The most accessible stands of Municipio Puerto Vallarta have been excessively tapped. Protuberances cover the trunks where cuts have penetrated through the cambium. Some trees have died and others have sections of the trunk in various stages of decay, but a remarkably large percentage of those severely tapped are healing up.

Tapping has been done in a haphazard manner with various tools. Usually alternate diagonals are slashed on the sides of the tree. The space between these varies greatly depending upon the condition of the trunk. The diagonals usually are not joined, and the latex flows from one to another until it reaches the base of the tree where it is collected in bamboo containers. Tappers have no regular schedule or assigned stands. Inquiries indicate that the trees are retapped at two-week intervals.

The trees give an estimated average yield of about 200 cc. of latex per tapping. The latex coagulates naturally overnight, or immediately upon the addition of water. Gum is prepared for market both in sheet and block form. For the preparation of sheets, blocks are chopped up, the gum pieces placed in hot water until soft, and then laminated. Sheets are shade dried for about three days before packing in henequen sacks.

The stands in the Municipio Puerto Vallarta could yield an estimated 700 tons of gum annually if fully exploited with a rational tapping system. A production of at least 200 tons annually should be possible from the stands in Nayarit and Sinaloa.

With continued unregulated exploitation, the wild stand of *C. tepiquensis* will be decimated within a decade.

**Cnidoscolus tomentosus** Lundell, sp. nov. Frutex, hirtellus et stimulosus. Folia petiolata, petiolo ad 9.5 cm. longo; lamina ad 12 cm. longa, 16 cm. lata, cordata, supra pilosa, subtus tomentosa, lobis 3 vel 5, paucidentatis. Inflorescentiae parvae. Capsula 1.6 cm. longa, stimulosa. Semina 10.5-11.5 mm. longa, 7-8 mm. lata. Caruncula 3.5-4.5 mm. lata.

Shrub; twigs stout, densely hirtellous at first, armed with stinging hairs up to 5 mm. long; pith with transverse plates. Petioles stout, costate, shorter

than the blade, up to 9.5 cm. long; the gland at apex of petiole fleshy, conspicuous, suborbicular. Leaf-blades broader than long, up to 12 cm. long (from apex of petiole), 16 cm. wide, the basal sinus rounded, open, the primary lobes and veins 3 or 5, usually 5, densely pilose on upper surface, tomentose on lower surface, with scattered short stinging hairs on upper surface and along margin, the stinging hairs absent on undersurface at maturity; the lobes extending to middle of blade, oblong or obovate-oblong, the margin of lobes subentire or dentate with 1-several remote acuminate teeth, the teeth up to 1 cm. long, mostly above middle of lobes, and at base of blade. Inflorescence (in fruit) small, 6 cm. wide, the peduncle thick, 11 cm. long, densely hirtellous, the short stinging hairs few and scattered; the primary branches 2, forked, with indument like that of peduncle. Staminate and pistillate flowers not seen. Capsules about 1.6 cm. long, sparsely pubescent, beset with short stinging hairs. Seeds oblong-ellipsoid, somewhat flattened, 10.5-11.5 mm. long, 7-8 mm. wide, conspicuously mottled at first, nearly black at maturity, truncate and slightly emarginate at base, acutish at apex; caruncle fleshy, large, 3.5-4.5 mm. wide, with two triangular wings, cordate at base, extending to below the small depressed hilum.

MEXICO: OAXACA, Santa María del Tule, October 17, 1943, *Efraim Hernandez X. s. n.* (TYPE in the herbarium of Southern Methodist University); vernacular name, *mala mujer*.

*C. tomentosus* was collected in the same locality as *C. Hernandezii*, and bears a resemblance to that species. It differs at once in having petioles glandular at apex, larger seeds with dissimilar caruncle, and sparsely pubescent capsules.

**Cnidoscolus velutinus** Lundell, sp. nov. Frutex, ca. 4 m. altus, pilosus et stimulosus. Folia longe petiolata, petiolo ad 37 cm. longo, stimulosus; lamina cordata, ad 28 cm. longa, 43 cm. lata, velutina, lobis 5, obovatis, remote dentatis. Sepala ♂ velutina, alba, 14-17 mm. longa. Stamina 10, 9-11 mm. longa, biverticillata. Sepala ♀ velutina, libera, 8-12 mm. longa, ad 5 mm. lata. Ovarium pubescens. Capsula ca. 12 mm. longa. Semina oblongo-ellipsoidea, ca. 9 mm. longa, 5.5 mm. lata. Caruncula 3 mm. lata, basi cordata.

Shrub, about 4 m. high; twigs thick, short pilose and beset with slender stinging hairs up to 5 mm. long; pith with transverse plates. Petioles stout, costate, pilose with rather firm hairs, beset with stinging hairs, up to 37 cm. long; gland at apex fleshy, shallowly lobed. Leaf-blades up to 28 cm. long (from apex of petiole), up to 43 cm. wide, deeply cordate at base, the sinus broad and rounded, the primary lobes 5, persistently velutinous on both surfaces with soft short hairs, the indument dense on lower surface, beset with few scattered hairs on upper surface and along margin; lobed to below the middle of blade, the apical lobes obovate, cuspidate, the sinuses narrow but rounded and open, the margin of upper two-thirds of lobes cuspidate-dentate with rather remote conspicuous teeth, the base of lobes dentate with smaller remote acute teeth. Inflorescence 4-13 cm. wide, the peduncle stout, 7.5-21 cm. long, the peduncle and branches densely velutinous, beset with few scattered stinging hairs or unarmed. Staminate flowers white; calyx velutinous, 14-17 mm. long, the tube comparatively slender, lobes short, broadly ovate-elliptic; stamens 10, in two whorls, 9-11 mm. long, basal 1.5 mm. of staminal column pubescent; lower (outer) stamens with filaments fused for 4 mm., free part of filaments about 2.5 mm. long; upper (inner)

stamens with filaments fused for 6 mm., free part of filaments about 3 mm. long; anthers 2.2–4 mm. long; staminodia 3, filiform, 4.5 mm. long. Pistillate flowers solitary in the forks of the branches, rarely geminate, pedicellate; calyx velutinous, lobed to the base, the lobes oblong or oblong-elliptic, 8–12 mm. long, up to 5 mm. wide; ovary yellow, pubescent; styles united at base, multilobed, sparsely hirtellous. Capsules broadly ellipsoid, about 12 mm. long, pubescent and beset with stinging hairs. Seeds brown, oblong-ellipsoid, slightly wider above center, about 9 mm. long, 5.5 mm. wide, with a narrow but conspicuous dorsal ridge, apex acutish; caruncle fleshy, 3 mm. wide, cordate at base, the lobes extending to or below hilum, the margin thick and smooth.

MEXICO: GUERRERO, near Xaltianguis, kilometer 407 of highway, on mountain side, October 20, 1943, *C. L. Lundell & Amelia A. Lundell 12592* (TYPE in the herbarium of Southern Methodist University).

*Lundell & Lundell 12592* agrees rather closely with the brief original description of *C. multilobus*, but differs significantly in technical details from the interpretation of the species by McVaugh (1943). Since the more detailed study of McVaugh presumably is based upon a reinterpretation of type material, there is ample reason for considering that an undescribed species is represented.

The caruncle of *C. velutinus*, cordate at base and with thick rounded edges, is altogether different from the caruncle described and figured by McVaugh (1943, fig. 13) for *C. multilobus*.

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## GLANDULAR LEAF HAIRS OF ORIENTAL TOBACCO<sup>1</sup>

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### INTRODUCTION

Numerous studies of plant hairs or trichomes have been made. Interest in these structures in the past appears to have remained largely academic, although certain studies that deal with cotton constitute a notable exception. Be that as it may, the studies which are summarized in a monograph by Netolitzky (1932) have yielded a body of knowledge concerning the origin, structure, classification, physiology, and ecology of trichomes. It is strikingly apparent from perusal of this monograph, moreover, that certain investigators have emphasized structural differences as bases for classifying trichomes whereas others have laid stress upon functional differences.

Seemingly trichomes have been variously defined and delimited in botanical writings, but the term is generally understood to apply to *epidermal* outgrowths that are external to and may occur upon any of the above-ground parts of ferns (Pteridophyta) and seed plants (Spermatophyta). Plants that belong in other phyla and which, therefore, are not properly regarded as possessing an *epidermis* may not, in accordance with restrictions imposed by this interpretation, be said to have trichomes. According to this concept of the term, moreover, such hairs as may occur within the intercellular spaces of certain aquatic plants, as among certain Araceae and Nymphaeaceae, or as the elements projecting from the inner locule walls of young *Citrus* fruits, which give rise to the pulp sacks, and the root hairs of seed plants generally, are not properly designated as trichomes.

As defined by Weiss, in 1867 (Netolitzky 1932), "A plant hair is a direct prolongation of an epidermal cell; it arises *externally*,<sup>2</sup> is thread-like, branched or unbranched, and consists of one or more similar or dissimilar cells." As characterized by de Bary (Netolitzky 1932), ten years later, trichomes are projections from and extensions of the upper wall of epidermal cells from which they have their origin. In the concept of Netolitzky

<sup>1</sup> These researches and those upon which a previous report was based were subsidized in part by the General Education Board. The previous report (Wolf and Jones 1944) dealt with the structure of green leaves of oriental varieties of tobacco at different stalk positions in relation to quality of cured leaves.

The constructive criticism of Drs. P. M. Gross and F. R. Darkis is gratefully acknowledged.

<sup>2</sup> Netolitzky (l. c., p. 7, 147) points out that part of the "druse" hairs of *Pogostemon* (Labiatae) extend outward and others inward, and therefore that it seems absurd not to regard both structures as hairs. (Some might be inclined to question the use of the term druse to apply to glandular hairs.)

(1932), more emphasis should be placed upon function than upon structure, for he states that trichomes are *epidermal organs*, i.e., *not mere appendages*, of characteristic structure that aid or enhance the epidermis better to function in protection, absorption, secretion, or storage, or to serve as sense organs.

Species of *Nicotiana* and of such closely related genera as *Solanum*, *Petunia*, *Physalis*, and *Lycopersicum* have long been known to possess both glandular and non-glandular hairs. It appears that the use made by these plants of their own glandular-hair secretions is quite unknown. On the other hand evidence was presented in a recent report (Wolf and Jones 1944) indicating that the characteristic aroma of tobacco is traceable primarily to the resinous exudate from glandular hairs. Since aromas of oriental tobaccos are their most prized attributes, a knowledge of glandular hairs becomes of enhanced interest, especially to tobacconists and botanists. The purpose of the present report therefore is to contribute further observations relating to glandular hairs on *Nicotiana*, and, so far as seems warranted, to interpret these observations.

#### MATERIALS AND METHODS

In these studies both natural and artificial environments in which to grow plants were employed. Under the former conditions twenty-nine varieties and strains of oriental tobacco were grown in a field at the Tobacco Experiment Station, Oxford, N. C., during the 1944 season, and, under the latter, four varieties were grown under glass, at Durham, N. C., during the preceding winter and spring.

Seedlings of the varieties grown under glass were transplanted into a sandy loam soil placed in 4-inch, unglazed, earthenware pots. Here they grew slowly, and all the leaves, as they matured, beginning with the lowermost, were removed from analysis. The period of their removal extended over the interval February 14 to May 12. It became necessary to limit to six the number of plants analyzed in each of the four varieties because the making of analyses was so time-consuming.

Seedlings of all varieties grown in the field were transplanted during the second week of May. They were spaced  $5\frac{1}{2}$  inches apart in 20-inch rows. Fertilization and cultivation of the kind and amount best suited to them, as indicated by previous experience in the culture of oriental tobacco, were given these plants. Harvesting began early in July and terminated two months later.

Preliminary sampling indicated that the total hair population of each leaf on any plant grown outdoors, regardless of its level on the stalk, is quite the same, except for a few of the uppermost leaves. For this reason it was deemed satisfactory to select five representative plants of each variety



and to take, for the analyses, three leaves from the median region of each such selected plant. In varieties that exhibited small differences in hairiness between these five selected plants the number of plants analyzed was limited to five. If, however, the differences between plants were rather large, more than five plants, the number being determined by available time, were analyzed in a search for individuals with leaves having a greater than average hair population.

Results of the analyses, upon which this report is based, involved the use of more than 2000 leaves on each of which the hair population in ten places was counted. To do this the lower epidermis was stripped off for microscopic examination. Large strips of lower epidermis may be removed with facility if the leaf is held taut over a finger tip and torn toward the midrib or toward the base of the leaf. It is quite impossible, however, by the same technique, to strip off large pieces of the upper epidermis because the palisade parenchyma adheres so closely.

Five ample strips of the lower epidermis of each leaf examined were placed in a film of water on a microscopic slide with the outer leaf surface uppermost. A cover glass was not applied for the reason that if the hairs are permitted to stand erect they can readily be brought into focus for counting. The hairs in two arbitrarily chosen microscopic fields on each strip were counted, and the average of these ten counts was taken as the number of hairs per unit area of leaf surface. The determination of hairiness and of leaf area of the tobacco varieties therefore rested upon two measurements: (1) an average of ten direct counts of hairs under low power magnification, using such combination of lenses that the area of the microscopic field was 1.0936 mm.<sup>2</sup>; and (2) a computed determination of leaf size. The size of a leaf was determined by tracing it to make a paper pattern which was, in turn, weighed and compared with the weight of a standard made from the same kind of paper. The weight per unit area of the standard had previously been determined. From the figure representing the number of hairs per mm.<sup>2</sup> on the lower leaf surface and the figure representing the calculated leaf area, the hair population per leaf was derived.

Hairiness, as used throughout this report, applies to the hair population on the lower leaf surface only. It was found possible, however, to determine hair population on both the upper and lower leaf surface of one and the same leaf. To do this leaf fragments were dehydrated by passage through graded concentrations of ethyl alcohol, after which they were cleared in methyl salicylate. When this was done the number of hairs per unit area on each surface, first on one side of the leaf fragment, then on the other, could be determined. By this technique it was found that the number of hairs on the upper leaf surface is approximately 20-25 per cent greater than on the lower surface.

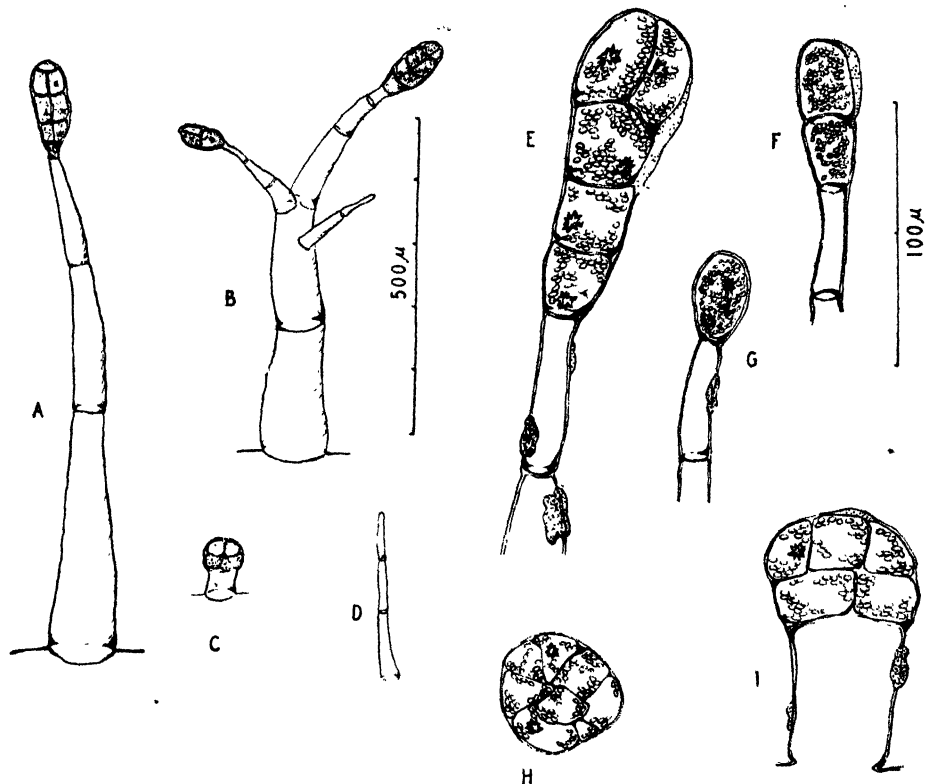
It is recognized that these methods of analyses permit errors of appreciable magnitude to be made, an eventuality that appears unavoidable for the following reasons: (1) Glandular hairs are not uniformly distributed over the leaf surface. Their distribution appears to follow the pattern of leaf expansion, as described by Avery (1933) in studies of growth of tobacco leaves. The hair population tends to be densest in areas of least expansion. Then of course, it becomes quite impossible to strip off the epidermis from exactly the same region of each leaf. (2) It is difficult or impossible to trace the leaf patterns exactly. In addition, (3) differences in relative humidity of the atmosphere on different days, with consequent differences in moisture content of the paper, introduce errors in the weighing of paper patterns. Furthermore (4) there was a ponderable lack of uniformity in the paper used for tracing. In spite of these obvious deficiencies in methods, the data are regarded as serviceable approximations, useful in comparing the hairiness of any two plants of one variety and also in comparing the hairiness of different varieties.

#### STRUCTURE OF GLANDULAR HAIRS

A variety of structural complexity is exhibited by the glandular hairs occurring on *Nicotiana*. Those of simplest design, when young, are composed of a single, cylindrical basal or stalk cell and a single, spherical or ellipsoidal, apical gland-cell (fig. G). As a result of elongation of this stalk-cell and the development of horizontal cross walls the stalk may become multicellular although the apical cell may remain unicellular. On the other hand, the apical cell may become multicellular by the formation of horizontal walls only, or of anticlinal and periclinal walls also (figs. C, H, S), while the stalk cell may remain unchanged (figs. C, I), or, as another alternative, both basal cell and apical cell may coincidentally become multicellular (figs. A, B, H, I). Occasionally branched hairs, having a gland at each tip, are formed (fig. B).

It seems proper to consider glandular hairs of *Nicotiana*, regardless of the simplicity or complexity of their design, as *special organs*, for the following reasons: (1) Within each such gland are several green plastids. By appropriate microchemical tests it may be demonstrated that the color is imparted by chlorophyll. The presence of chlorophyll was demonstrated by removing the hairs, treating them while on a microscopic slide with 25 per cent HCl or glacial acetic acid, then heating the preparation to 90° C, whereupon, after a brief period, long brown needle crystals, that were soluble in ether or chloroform, were produced. The presence of chloroplasts within the glands makes possible the elaboration within them of photosynthetic products that could, in turn, be utilized *in situ* in chemosynthetic processes. Such a condition is by no means unique, because chlorophyll-bearing hairs are

known to be not uncommon among plants. For example, as long ago as 1882, Haberlandt (Netolitzky 1932, p. 48) noted chloroplasts in the hairs of *Rubus odoratus* L., *Melandryum viscosum* Čelak., and *Urtica dioica* L. He gave the name "lokalassimilatorischen Zellen" to such glands because they are sepa-



FIGS. A-I. Hairs of oriental tobacco. Figs. A, B, C, and D drawn to one scale; Figs. E, F, G, H, and I to the other. FIG. A. Glandular hair having three stalk cells and multicellular gland that is divided by planes at right angles to each other. FIG. B. Branched glandular hair. FIG. C. Short glandular hair with one stalk cell and many-celled gland. FIG. D. Trichome lacking gland. Some hairs appear never to become glandular and from others the gland may become dislodged. FIG. E. Tip of glandular hair. The gland cells contain chloroplasts and crystals. Exudate has accumulated beneath the cuticle. Droplets of exudate have lodged on the stalk. FIG. F. Two-celled gland with accumulated exudate beneath cuticle. FIG. G. One-celled gland with droplet of exudate adhering to stalk. FIG. H. Short-stalked multicellular hair as seen from above. FIG. I. Hair of the same kind as in figure H, when viewed from the side.

rated by chlorophyll-free cells from the assimilatory tissue (chlorenchyma, in leaves) and because they elaborate substances of a special kind.

(2) Crystals that are generally conceded to be by-products of metabolic processes, i.e., of respiration and perhaps also of synthesis of resinous substances by *Nicotiana*, occur within the gland cells, as revealed by direct

microscopic examination (figs. E, G, H, I). As long ago as 1888, Wakker (Netolitzky 1932, p. 49) drew attention to the presence of crystals within tobacco hairs. These crystals are to all appearances of the same kind as those within leaf mesophyll.

(3) The wall of the gland cell or cells is composed of two distinct membranes, the wall proper and a cuticular tegumen or cuticle. The former is mainly cellulosic as demonstrated by reaction with chloriodide of zinc, and the latter is cutinized, as indicated by reaction with Sudan IV. Apparently as the resinous materials (a mixture of waxes and ethereal oils) are elaborated and secreted, they accumulate between the wall and the cuticle to form a bleb. Eventually the secretions have accumulated in such volume as to rupture the cuticle, whereupon they appear external to the hair as droplets or as films that adhere to the hairs (figs. E, G, I) or spread out over the leaf surface. The wall proper remains intact, however, and the gland may continue for an indefinite period to synthesize and secrete the resinous exudate. Observations indicate that leaves are mature, and hence prime, at a time corresponding with that of greatest glandular activity. Proof of such correlation must remain lacking, however, until methods for measurement of leaf maturity and of rate of glandular activity have been perfected.

Whether the secretions from glandular hairs of tobacco *early* accumulate in blebs, as described above, or whether the blebs form *late* remains, however, a controversial matter. Tunmann in 1913 and 1914 (Netolitzky 1932, p. 149<sup>3</sup>) held that they do not form blebs early. He classified glandular hairs as oil druses, fat druses, and wax or resin druses. He stated that the hairs of *Nicotiana* and other Solanaceae are examples of the latter kind, and that the waxes are emptied to the exterior as rapidly as they are formed. Secretion by fat druses takes place in a similar manner, according to him. Chodat (Netolitzky 1932, p. 152<sup>4</sup>) concluded that the secretions of *Nicotiana* might be regarded as myelin, i.e., fatty materials, hence he would regard the glandular hairs as fat druses.

Feher (1923), from studies of resin secretion by *Populus*, came to the conclusion that there is no accumulation of secretion between the cuticle and cellulosic wall so long as the former remains permeable. When finally the gland wall becomes impermeable, however, then the cuticle is raised up, and the pressure exerted on it could eventually cause its rupture. On the other hand, Klug (1926) found that the oily secretions by *Mentha piperita* accu-

<sup>3</sup> "Wir müssen bis jetzt, wenn wir von den Kollateren und den Schleimdrüsen absehen, unterscheiden: Öldrüsen, Fettdrüsen, und Harzdrüsen. . . . Bei den Fettdrüsen . . . sammelt sich die Sekret nicht subkutikulär an, sondern wird sofort nach aussen entleert. Zu den Harzdrüsen gehören beispielsweise die keulenförmigen Drüsen der Solanaceen. Bei diesen findet ebenfalls keine subkutikuläre Ansammlung statt, das gebildete Harz wird sofort nach aussen entleert."

<sup>4</sup> "die Ausscheidung der Drüsen von . . . *Nicotiana* die wohl auch nur als Myelinbildung gedeutet werden können."

multate beneath the cuticle to make, at maturity, bladder-like vesicles, and that such secretions could be dissolved out to leave the cuticle intact.

It is found that oriental tobacco leaves possess their entire complement of hairs by the time they are from one-fifth to one-fourth their mature size. This fact was established from a series of determinations of total hair population on expanding leaves, employing for this purpose "bud" leaves that were destined to occupy the median stalk region.

#### DEVELOPMENT OF HAIRINESS

In a previous report (Wolf and Jones 1944) the conclusion was drawn that each leaf on any given plant of oriental tobacco tends to have the same hair population. The data upon which this conclusion was based were secured from examination of leaves selected at random from consecutive primings of

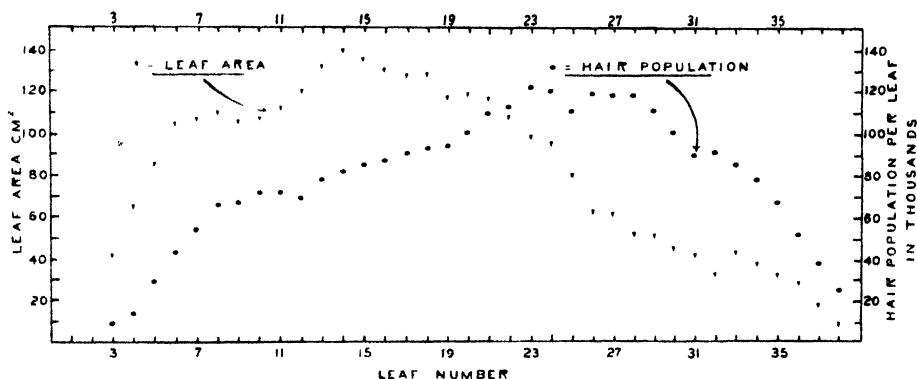


FIG. 1. A composite graphic portrayal of leaf size and total hair population of four varieties of oriental tobacco grown under glass during winter and early spring.

each of four varieties. It seemed that this conclusion would be more decisively established were one to use, in sampling, a sufficient number of selected plants from which every leaf was removed for analysis. Accordingly four varieties were employed in such an analytic study, but the number of individuals of each kind was perforce limited to six. These plants were grown under glass during the winter and spring of 1943-1944, as previously indicated. They were transplanted into porous, earthenware pots, but in so doing the first and second leaves were destroyed. However, the hairiness of similar leaves on seedlings that were not transplanted and also of cotyledons on such seedlings were determined. As regards cotyledons, it was found that they entirely lack hairs. As regards the first true leaf, it was found that it bears few hairs, and that these hairs are restricted, for the most part, to the principal veins and leaf margins. A considerably larger number of hairs occurs upon the second leaf, however, than upon the first one.

As each leaf above the first and second ones matured it was removed for determination of leaf area and hair population. An average was made, according to leaf position, of these determinations for each of the four varieties. Then from these averages a composite figure for all leaves of corresponding position was derived. Pertinent data from these composite figures are presented graphically in figure 1. It is apparent from figure 1, first of all, that under the conditions of these experiments, each leaf on any given plant is not equally hairy. Instead hair population tends to increase rapidly and progressively with increase in level of attachment until approximately the eighth leaf. It may be recalled, at this juncture, that the lower six to eight leaves are usually not included among harvestable ones when oriental

TABLE 1. *Differences in leaf size and hair population between field-grown and greenhouse-grown oriental tobaccos.*

Variety	Location grown	Average leaf area, cm. <sup>2</sup>	Average number hairs per leaf in thousands	Average number hairs per cm. <sup>2</sup>
Ayassolouk	Field	147.6	183.2	1240
	Greenhouse	123.3	101.7	825
Broussa	Field	149.6	259.2	1734
	Greenhouse	92.6	105.5	1140
Izmir	Field	131.2	159.5	1215
	Greenhouse	88.8	70.7	796
Stanimaka	Field	152.0	205.3	1350
	Greenhouse	115.0	119.6	1040

tobacco is grown in the field. Throughout a region above the eighth leaf, and extending to the twenty-eighth, the trend of increasing hair population per leaf continues but it is quite gradual. The difference in number of hairs on leaves nearest each other throughout this region is slight. With further progression along the uppermost region, however, each leaf may have a lesser number of hairs, a decline that may be related causally to nutrition. Difference in hairiness as displayed by leaves at different levels on greenhouse-grown plants is plainly at variance with findings when these same varieties of tobacco were grown in the field during the previous year (Wolf and Jones 1944). Moreover the number of hairs per leaf of plants grown under glass is strikingly less than that of plants of the same varieties grown in the field. A reason for these discrepancies was therefore sought by again analyzing hairiness on these varieties, when grown in the field. Resultant data on comparative varietal differences in average hair population and in leaf size of plants grown under glass and of plants grown outdoors are shown in table 1.

It should be recalled in interpreting the data in table 1 that each plant of any given variety of oriental tobacco tends to bear the same number of leaves, i.e., that fixity in leafiness is a varietal characteristic. Fixity of leafi-

ness, moreover, tends to be maintained regardless of the environment. In each of the four varieties, in table 1, larger leaves having a greater population of hairs were produced when the plants were grown in the field than when grown indoors. These data on leaf-size differences indicate that leaves on plants grown in the field may range from 20 to 60 per cent larger than those grown under glass, that the former has a greater hair population per unit area, and that they may have from 70 to 140 per cent more hairs per leaf. What is more significant than these differences is the fact that on field-grown plants each leaf on any given plant tends to have the same total hair population. It would seem therefore that an interpretation of these differences in hairiness must assume that hairiness is conditioned by two fundamental factors, one hereditary and the other environmental. If hereditary factors alone were operative hair population should tend to be the same regardless of environment. The fact that the upper leaves tended to become more and more hairy with the advance of spring when plants were grown indoors, and that they tended to be uniformly hairy when plants were grown in the field, seems to be due predominantly to environmental factors, presumably light. Further consideration of the matter of environmental effects on hairiness, however, will be given subsequently in this report.

#### HAIR POPULATION ON LEAVES OF DIFFERENT VARIETIES OF TOBACCO

That different varieties of oriental tobacco are preceptibly different in density of hair population is apparent even from quite casual observation. Manifestly the scope of these differences can be appreciated only if data on comparative measurements are available. The present purpose therefore is to express these differences numerically and thus, at the same time, to determine whether a basis exists for attempts to increase hair population per unit area by selection. All varieties considered herein were field-grown under as nearly as possible similar conditions of spacing, fertilization, and cultivation. It should also be borne in mind that all parent plants grown during the four preceding seasons had been bagged to prevent hybridization of varieties. The results of analyses of varietal differences are portrayed in table 2.

Among the varietal differences in hairiness shown in table 2, three are outstanding. First, the hair population per leaf may range from less than 100,000 to over 500,000. Second, within certain varieties there is a narrow range of difference in hair population between individuals, whereas in other varieties the leaves of certain plants have 50-100 per cent more hairs than do others. Third, there is a wide range in hair population per unit area of leaf surface, for some varieties have approximately twice as many hairs per unit area as do others. These differences would indeed have significance if, by selection of seed plants with greatest density of hairs, the average hairiness could be increased, since thereby the volume of aroma should also be in-

creased. Work of selection, to test this possibility, is in progress and the results should appear in a subsequent report.

TABLE 2. *Varietal differences in field-grown oriental tobaccos.*

Type	Time of maturing	Varietal name	Number leaves per plant	Average number hairs per cm. <sup>2</sup>	Average leaf area per cm. <sup>2</sup>	Total hair population per leaf in thousands			Range of hairiness as per cent
						Average	Maximum	Minimum	
Samsoun	Early	Persician (Prosetchan)	22-24	969	215.8	206.0	240.3	153.6	42.1
	Early	Samsoun	28-30	921	153.7	183.6	206.9	156.9	40.9
	Late	Broussa	38-45	1758	149.6	259.2	289.9	241.9	18.4
	Early	Samsoun (E)	26-28	1189	144.1	165.6	185.5	161.2	14.1
	Late	Dere	35-40	1438	179.9	255.7	327.5	200.4	49.7
	Median	Samsoun (G)	28-30	1440	113.9	158.7	201.1	128.0	51.7
	Late	Katarini	36-38	1201	130.3	142.4	189.3	92.2	68.2
	Late	Katarini (M)	36-38	1054	231.7	233.1	279.9	198.1	35.1
	Late	Katarini (W. L.)	36-38	1604	125.1	198.9	217.3	179.6	18.5
Smyrna	Late	Izmir	35-40	1222	131.2	159.5	199.3	151.4	29.6
	Late	Smyrna	28-30	1770	143.7	245.0	267.7	235.0	13.3
	Late	Ayassolouk	39-46	1267	147.6	183.2	331.9	115.6	118.0
Cavalla	Late	Jalomita	21-24	1397	362.5	502.5	599.3	431.9	33.5
	Early	Molovata	24-28	942	244.5	227.9	272.8	195.6	33.9
	Median	Ghimpati	26-30	1307	188.5	243.4	284.7	208.8	31.1
	Median	Stanimaka	33-36	1385	152.0	205.3	250.6	184.9	29.9
Xanthi	Early	Dragasani	22-24	869	134.6	114.4	126.7	85.7	35.8
	Early	Xanthi-Yaka (R)	22-24	996	137.0	135.2	143.3	132.1	8.2
	Early	Xanthi-Yaka (G)	22-25	878	93.4	82.0	90.1	64.4	30.3
	Median	Ustina 60	24-28	1266	144.9	181.8	233.8	150.4	45.9
	Median	Ustina 45	27-30	1350	179.2	234.6	281.3	173.8	45.8
	Median	Ustina 42	27-29	1387	148.1	197.9	242.9	147.8	48.0
	Early	Yenidge	23-25	1019	148.0	149.3	159.8	134.8	16.8
	Early	Yenidge 134	20-24	1166	138.1	152.4	202.4	133.6	55.0
	Early	Djebel	20-24	1099	92.4	99.6	105.5	92.3	13.2
	Early	Xanthi-Yaka (G2)	22-24	1723	66.9	114.3	124.8	97.7	23.7
	Early	Hendek	27-32	990	182.6	178.7	202.8	144.7	32.5
	Early	Goli Ruchki	21-24	904	149.7	140.1	202.5	82.3	83.7
	Early	Stob	21-24	885	165.6	143.4	189.3	92.1	68.2

It is believed that significance should be attached to date of maturity in interpreting the data in table 2. Those varieties having 20-24 leaves tend to mature early, those having approximately 30 leaves tend to mature at mid season and those having 35 or more leaves are late-maturing. Observations



on these varieties may be interpreted to show that tobacco of most satisfactory yields and with best quality have been secured from kinds that mature late, have the largest per unit area hair population, and produce leaves of median size. In any event, hairiness seems to be a tool that may be used in evaluating oriental tobacco prior to curing.

Attention might well be directed to a feature associated with each of these varieties of oriental tobacco, namely the existence of differences in aroma. Some varieties have very distinctive odors even before the leaves are primed. The causes of these differences are quite unknown but seemingly should be related to differences in proportion of ethereal oils and waxy materials of which the exudate is composed.

#### DECLINE IN HAIR POPULATION OF UPPERMOST LEAVES

It is well appreciated by tobacconists that, with oriental tobacco, cured leaves of poorest quality are usually obtained from the first priming, and

TABLE 3. *Trend in leaf size and hair population of the uppermost leaves of field-grown tobacco, Ayassolouk variety.*

Leaf position	Average area cm. <sup>2</sup>	Average num- ber hairs per cm. <sup>2</sup> in thou- sands	Average num- ber hairs per lower leaf sur- face, in thou- sands
Top leaf	15.2	3.5	53.7
2nd leaf from top	20.2	3.3	65.0
3rd leaf from top	29.8	3.2	97.0
4th leaf from top	35.3	2.8	100.6
5th leaf from top	41.4	2.7	112.5
6th leaf from top	45.3	2.6	120.2

that usually with each successive priming thereafter the quality of the crop improves. In some cases, however, tobacco of best quality is not produced from leaves along the uppermost stalk region. Unfavorable weather near the close of harvest, especially excessive rainfall or extreme drought, are conceded to contribute causally to decline in quality. Whether, as a proximate causal factor, decrease in hair population is correlated with decline in quality of uppermost leaves was given consideration, with the results shown by data in table 3.

Two facts are obviously established by the data contained in this tabulation. (1) Total leaf size and total hair population per leaf increases from the top leaf downward quite uniformly; and, as must follow, (2) with increase in leaf size, the hair population per unit area tends to decrease quite uniformly. The rate of subsequent change with downward progression is shown by the fact that unit-area population on the sixth leaf is approximately twice that of the average leaf of the variety Ayassolouk as shown in table 2.

That decline in quality of uppermost leaves is actually correlated causally in any case with decrease in total hair population seems highly improbable, however. This statement may at first seem to contradict the underlying correlation of hairiness and aroma. Even though these uppermost leaves have the larger glandular hair population per unit area, and therefore may be presumed to be more aromatic, yet quality undoubtedly depends upon such other factors besides hairiness, as leaf texture, size of component cells, compactness of constituent cells, chemical composition (both organic components and minerals), maturity of leaves when primed, proper curing, and proper subsequent manipulation.

The proximate causes of decline in hair population of leaves near the top of the stalk remain wholly unknown. It seems probable, however, that these causes are related to senility of the plant as a unit and to modification of physiological processes within these uppermost leaves as influenced by priming, nutrition, and other factors.

#### EFFECTS OF SPACING

The cultural practice of close-spacing, as employed in growing oriental tobacco, intensifies competition between individuals for water, nutrients, and light. The intensity of this competition is reflected by degree of resultant dwarfing. It seemed probable that hairiness might also be affected by competition, at least in some degree commensurate with such gross structural features as change in size of plants and size of leaves. In attempts, therefore, to measure influence of spacing on hairiness, three varieties of tobacco, an oriental, a flue-cured, and Burley, were transplanted into the field in such manner that there were eight times as many individuals per unit area of land in plots having closely spaced plants as in those having widely spaced ones. The same amount of manure per unit area of land was applied before transplantation, except that to the plot with widely spaced flue-cured plants supplementary inorganic nitrogen and phosphorus were added. As selected plants in these plots approached maturity, all their leaves were harvested for analysis, and the results have been summarized in table 4.

Under these conditions the average total leaf area of a widely spaced plant was from two to three times greater than that of a closely spaced one and each plant of the latter kind had approximately 60-75 per cent as many hairs as the former. The average size of leaves on closely spaced plants was approximately half that of those on widely spaced ones; then too, the average number of hairs per leaf on closely spaced individuals was very materially smaller. The density of hair population was, of course, correspondingly greater on the closely spaced plants. These differences in hair population and density between corresponding sets of plants cannot be ascribed to any single factor comprising the spacing complex. The experiments with ferti-

lizer materials, next to be presented, constitute an attempt to isolate the environmental factors that interact in spacing. In any such studies it seems reasonable to suppose that a pattern of hairiness exists, and that environmental factors operate through a fixed pattern of hairiness. By this connotation is meant that the ratio between epidermal cells having glandular hairs and those lacking them, tends to be fixed by mechanisms internal to the leaf, but that control of orderliness in this design may be disturbed within a limited range by external factors. Evidence that tends to support this concept appears from results, that follow, of experiments to isolate the nutritional factor.

TABLE 4. *Influence of spacing on hairiness.*

Variety of tobacco	Spacing	Average total leaf area per plant, cm. <sup>2</sup>	Average total number hairs per plant on lower leaf surface in thousands	Average size of leaves, cm. <sup>2</sup>	Average number hairs per leaf on lower leaf surface, in thousands	Average number hairs per cm. <sup>2</sup> on lower leaf surface, in thousands
Ayassoulouk	Widely Spaced	8,037	8,647.8	254.3	273.7	1.1
	Closely Spaced	3,320	5,743.6	114.5	198.1	1.7
White Burley	Widely Spaced	12,350	13,574.8	617.6	678.7	1.1
	Closely Spaced	6,870	8,459.9	343.9	423.0	1.2
Flue-cured No. 401	Widely Spaced	11,790	18,435.5	539.4	927.8	1.7
	Closely Spaced	4,510	10,106.9	225.4	505.3	2.2

## INFLUENCE OF FERTILIZER ON HAIRINESS

Even though a complex of interacting factors that are quite inseparable was concerned in the foregoing experiments with spacing, nevertheless partial separation of the nutritional factors was sought by comparing the effects on hairiness of application of a fertilizer, almost entirely organic, with one, almost entirely inorganic. These experiments involved plants grown closely-spaced. The results secured are assembled in table 5.

In explanation it may be stated that growth was more rapid and the plants were larger in the case of those supplied with inorganic nutrients. This difference is reflected in the average leaf sizes which were approxi-

mately 250 cm.<sup>2</sup> and 340 cm.<sup>2</sup> for plants grown with organic fertilizer and with inorganic fertilizer, respectively. The numbers of hairs per unit area of lower leaf surface were essentially identical in the two cases, being 1694 and 1709, despite the fact that the average size of leaves from plants supplied with inorganic fertilizer was 34.7 per cent the greater and the average hair population was 36 per cent the greater. From these results it seems reasonable to assume (1) that leaves of both groups of plants possessed equal numbers of non-hair-bearing, epidermal cells, (2) that a proportionality between hair-bearing and non-hair-bearing epidermal cells was maintained in each case, and therefore (3) that the larger size of component cells and not

TABLE 5. *Influence of fertilizer on hairiness.*

Environment	Average leaf area, cm. <sup>2</sup>	Number hairs per cm. <sup>2</sup>	Average number hairs per lower leaf surface
OS and OF	253.5	1,694	429,429
OS and FF	341.8	1,709	584,136

OS = Plants spaced closely as is done with oriental tobacco.

OF = Fertilizer of a kind (organic) known to be suitable for oriental tobacco culture.

FF = Fertilizer of a kind (largely inorganic) known to be suitable for flue-cured tobacco culture.

greater number of cells accounted for the larger size of leaves on plants supplied with inorganic fertilizer.

#### INFLUENCE OF LIGHT ON HAIRINESS

No experiments have been attempted to evaluate decisively the extent to which light affects hairiness. However, in connection with the results in figure 1 which portray progressive increase in hair population with advance of the season, as has been indicated previously, it seems reasonable to ascribe this increase to light as a prime causal factor. Some support for this conclusion stems from an analysis of these composite figures showing leaf size and hair population. The group of largest leaves, 12-16 inclusive, was harvested during the period April 7-13. The group of leaves, 23-28 inclusive, possessing the largest hair population, was harvested May 17-26. Manifestly quite different light conditions prevailed, during the critical period of early expansion of those groups of leaves. The average leaf area of the former group is approximately 130.6 cm.<sup>2</sup> and hair population 79.5 (in thousands); corresponding average figures for the latter group are 71.3 cm.<sup>2</sup> and 117.5 (in thousands) respectively. That light induces responses through a numerical pattern between hair-bearing and non-hair-bearing cells is unknown in this instance, and such possibility must await determination. Evidence that response of this sort occurs rests, at present, mainly upon the fact that hair

population of a given leaf becomes fixed by the time the given leaf has attained from one-fifth to one-fourth its mature size.

#### SUMMARY

That aroma arises primarily from exudate of glandular hairs was concluded from previous studies of the structure of leaves of oriental tobacco. It seemed desirable, therefore, to acquire more knowledge of hairs, herein regarded as secretory organs, to serve as a basis for attempts to increase hairiness, and thereby to increase the volume of aroma. To this end studies were made both of hair structure and of hairiness.

The gland cell or cells contain chloroplasts, as has been reported by others. These photosynthetic structures are lacking, however, in the stalk cells and in the epidermal cells from which glandular hairs arise. Chloroplasts within glands enable them to synthesize exudate *in situ* and eventually to excrete it. Elaboration and excretion of exudate may continue throughout the entire period that the leaf remains functional. The exudate from different varieties is quite unlike, as judged by the sense of smell. In fact, certain varieties possess an odor that is quite distinctive.

The density of hair population and total number of hairs per leaf differ according to the variety of oriental tobacco. The range in hairiness is rather wide, as shown by the fact that certain varieties have approximately twice as many hairs per unit area as do others. These characteristic varietal differences are not immutable however, but are subject to modification and control both by hereditary and environmental factors that act interrelatedly. Present observations indicate that partial separation of such interaction can be accomplished.

As regards findings that may be attributed to controls exerted by hereditary factors it has been noted (1) that differences exist in hair population per unit area of leaf surface and per entire leaf, when different varieties are grown under identical environmental conditions; and (2) that all individuals of certain varieties may have quite the same number of hairs per leaf whereas certain plants of other varieties may have approximately twice as many hairs per leaf as others.

Differences in hairiness between individuals that come from one and the same seed plant indicate that hairiness may be increased by selection. If such an eventuality were to be realized new strains having a greater volume of aroma should be the outcome.

As regards findings that seem traceable to controls induced under the influence of environmental factors the following have been noted: (1) Wide differences in hairiness occur within one and the same variety when grown under glass during the winter season and when grown in the field during summer. Plants grown during winter are much less hairy than those grown

during summer. Under the influence of wide variation in environment during early spring there was lack of uniformity of hair population per leaf whereas during the more favorable environment of summer each leaf had quite the same number of hairs. (2) Many more hairs per leaf are produced by plants of one and the same variety when grown widely spaced than when grown closely spaced. The leaves on widely spaced plants may be from two to three times larger than those on closely spaced ones; the per unit area population of hairs in the former case, however, is very markedly less than in the latter.

The number of hairs on leaves along the basal stalk region and near the tip is always different from that of leaves along the main portion of the stalk.

None of the interrelated factors, including nutrition, water, and light, involved in the experiments with spacing, has been resolved adequately. As having bearing on nutrition, observations indicate that tobacco plants grow more rapidly and are larger if they are supplied with readily available nutrients than if the nutrients are slowly available. Such larger plants with larger leaves have the greater total hair population. Determination of density of hairs on leaves, total hair population, and leaf area, indicate, for these two sets of plants, i.e., widely-spaced ones and closely-spaced ones, the existence of a pattern of hairiness. As having bearing on light, hairiness is increased with increased illumination.

Insofar as hairiness is correlated (1) with time of maturity of a given variety, (2) with leafiness, and (3) with desirable leaf size, it seems to be a criterion by means of which an evaluation can be made of the leaf prior to curing. It is indicated that further knowledge of environmental influences upon hairiness should be sought.

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CYTOPLASMIC HYBRIDS IN *PENICILLIUM NOTATUM*

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Derx (1925) mated the cultures from twelve single spores of *Penicillium luteum* in all combinations and Shear and Dodge (1927) state, "Derx . . . has proved conclusively that *Penicillium luteum* is heterothallic." Emmons (1935) has shown that single ascospores isolated from *P. luteum* produce perithecia but this does not invalidate Derx's conclusions, for closely related fungi are known to produce both homothallic and heterothallic forms. Since Derx proved the existence of heterothallism in some *Penicillia* we purposed to investigate the question of the existence of heterothallism in this so-called species.

*P. notatum* is a *form* species rather than a *truc* species. The fact that it is isolated rather frequently from nature is the only basis for giving it specific status and most systematists recognize that calling it a species is a necessary and useful violation of the species concept. It probably originated from *Penicillium* ascospores and is perpetuated in nature asexually. *P. notatum* is identified as a species only by its morphological characters and the structure of the penicillus suggests that it may be a degenerated form of a more vigorous parent. In *Neurospora* a vigorous, well developed conidial form may produce a large number of different kinds of much inferior progeny. It is possible that *P. notatum* is genetically sterile at its origin or that variation has altered the mating-type specificity and that it is incapable of producing hybrids. It may be significant that Derx mated the cultures which he obtained from single ascospores very shortly after having isolated them. If the same cultures had been tested a few months later they might have been incapable of producing perithecia. A parallel situation is found in yeasts. Lindegren and Lindegren (1944) have shown that haploid yeast cultures capable of copulating vigorously may lose their mating-type specificity and become completely sterile when carried in culture. Lindegren, Beanfield and Barber (1939) described variations in the fertility of *Neurospora* cultures.

Twenty-five cultures of *P. notatum* of the P. S. (*Penicillium Survey*) series collected from a variety of sources were obtained from Dr. Raper of the Northern Regional Research Laboratory. These cultures had all been dried *in vacuo* and sealed in glass tubes shortly after isolation. Cultures grown from these lyophil tubes were paired in 183 combinations on molasses-peptone-agar slants and carefully observed to see if perithecia were produced. No perithecia were found a month later, although *P. luteum* sporulated

abundantly on this agar within a week. This experiment seemed to limit or exclude the possibility of making true hybrids in *P. notatum*, so an attempt was made to produce heterokaryons between these different cultures. Foster, Woodruff and McDaniel (1943) have shown that *P. notatum* becomes heterokaryotic by mutation, with a rapid loss of penicillin-producing ability. They found that the new mutants which occurred in the mat seemed to decrease its capacity to produce penicillin.

Baker (1944) showed that the septations in *P. notatum* are perforate and that fusions between germinating spores and between different hyphae occur frequently. Her figures suggest that conditions in *Penicillium* may approximate those in *Neurospora*, in which heterokaryosis is extremely important, especially for survival in nature. Lindegren (1934) has shown that heterokaryosis is so advantageous to the filamentous fungi that it is probably the natural condition for all of them.

Hansen (1938) has described the "dual phenomenon" in a wide variety of fungi, and Hansen and Snyder (1944) have made observations on *P. notatum*, which they conclude also exhibits the "dual phenomenon." What Hansen referred to is obviously simple heterokaryosis. Previously to Hansen's work, both Dodge (1928) and Lindegren (1934) had shown that heterokaryosis is the rule in *Neurospora* and, furthermore, that the condition is not "dual" but multiple. The commonest type of mutation involves loss of the ability to produce conidia. Lindegren (1936) found at least ten different nonconidial mutants in *Neurospora*, all of which were non-allelic. To speak of a heterokaryon of conidial and nonconidial forms as a "dual phenomenon" oversimplifies the situation. The nonconidial mutants are easy to detect by observation. This is especially true in *P. notatum* and may be due to the fact, recently discovered by Pontecorvo and Gemmell (1944), that the nonconidial form may be dominant in the heterokaryon. However, in addition to nonconidial forms, natural heterokaryons contain a number of other types of mutants.

#### EXPERIMENTS

The first step in the formation of heterokaryons is hyphal fusion, and our first experiments were designed to test the readiness with which fusions occur between different cultures of *P. notatum* and to select strains which were able to anastomose readily. The fact that hyphae fuse has no significance from the standpoint of mating type or sexual difference. It is characteristic that some cultures are able to fuse more readily than others. In one mycelium fusions may occur readily between adjacent hyphae, while in another strain of the same species practically no fusions will occur.

The experimental procedure was as follows: Sterile slides were coated with a thin layer of nutrient agar and parallel streaks of conidia from a



single *P. notatum* culture were made on each slide with the inoculating needles adjusted so that the points were approximately 2 mm. apart. These slide cultures were allowed to incubate at room temperature (about 80° F). In most cases conditions were optimum for observation at 48 hours. Fusions between the hyphae could be observed in the region between the parallel streaks at 48 hours, but after the second day overgrowth generally obscured precise observations.

Three of the 25 N.R.R.L. strains of *P. notatum* showed a marked tendency to fuse, seven others did so with somewhat less vigor, and the remainder either demonstrated a pronounced reluctance to fuse or the mycelium failed to grow across the intervening space. In very few cases did fusions occur with any of the strains where the parallel streaks were more than 3 mm. apart. When the streaks were from 3 to 5 mm. apart the mycelia would advance to within about 1 mm. of each other and growth on the inner sides would cease, although it continued on the outside. The three N.R.R.L. strains, No. 49, No. 72, and No. 75, each of which had demonstrated a strong tendency to produce hyphal fusions with themselves, were matched in pairs on agar slides. The three possible pairings all exhibited abundant fusions after two days. This is exceptional, for in most other instances where the parallel streaks originated from two different strains, a pronounced barrage occurred.

When fusions occurred between two different strains a transfer was made to an agar slant and the resulting culture was studied carefully for uniformity. In no case were sectors observed, and the mycelium was always intermediate in roughness and other observable characters. Since the previous tests had shown that the mixed mycelia were compatible, we concluded that the combinations produced heterokaryons rather than fungal mixtures.

Hyphal fusion is not a mating-type or a sexual phenomenon and there is no apparent limit to the number of genotypes which can be built into one heterokaryon. A triple heterokaryon was made by mixing Nos. 72, 75, and 49.

Culture No. 72 (which was most compatible from the standpoint of penicillin production) was paired with two cultures which we had been using in the laboratory for penicillin production. Mat cultures of all the original strains and the heterokaryons were grown in penicillin-medium in 2-quart milk bottles. All tests were run in triplicate and many in quadruplicate. The results were averaged, and the agreement in all cases was rather close. Before seeding the heterokaryons, the mixed cultures were grown on agar slants. The bottles were inoculated and kept one day at room temperature and 7 days at 23° C. The filtrate from the bottles was assayed by the Oxford method, using glass cylinders on an agar plate sown with staphylococci. The amounts of penicillin in Oxford units are shown in the following table:

Strain	Penicillin	Strain	Penicillin	Strain	Penicillin
No. 49	20	No. 49	18	No. 20.4	50
72	47	72	90	40.1	5
75	25	75	22	72	33
49 & 72	12	49 & 72 & 75	2	20.4 & 72	35
49 & 75	7			20.4 & 40.1	5
72 & 75	47			40.1 & 72	27

Culture No. 49 has a definitely destructive effect on the penicillin production of cultures with which it is associated. No. 75 and No. 72 seem to be compatible, if not complementary. No. 72 and No. 20.4 also seem compatible.

#### HETEROKARYONS IN NATURE AND IN THE LABORATORY

Under natural conditions many conidia usually germinate together and if the strains are compatible anastomoses immediately produce heterokaryons. Therefore, in nature heterokaryosis is an especially favored condition and opportunity is afforded for continued increase in complexity of the thallus. However, laboratory manipulation of fungal cultures leads to a different end. On agar plates single conidia germinate separately and cultures are selected which are of monoonidial origin. Many of these cultures are homokaryotic, and this is especially true of fungi such as *Penicillium* which has uninuclear conidia. The high lability of penicillin production, as indicated by our experiments on heterokaryons, suggests that under natural conditions, where mixtures are the rule, little or no penicillin is produced. Only in the laboratory where homokaryons are handled, or when a single conidium falls in a plate (as in Fleming's original observation), can appreciable amounts of penicillin be expected. The possibility still exists, however, that the yield of penicillin may be increased by making mixtures. Dodge (1942), and Beadle and Coonradt (1944) showed that mutants deficient for certain physiological characteristics may mutually supply each other's deficiencies in a heterokaryon.

Because of our limited knowledge of sexuality in the *Penicillia* and *Aspergilli*, and the general conviction that with few exceptions these species are imperfect, attempts to improve penicillin production have been confined principally to the selection of supposedly imperfect cultures isolated from nature. But this program is very inflexible, for even if the isolation of a large number of different forms of *P. notatum* should yield exceptionally effective penicillin producers, improvement of the culture is limited by the potentialities of the original isolate because this so-called species apparently is incapable of mating and our own attempts at improvement by cytoplasmic mixtures do not show too much promise.

The fact that some penicillin producers are still using their original cultures indicates that an extensive search has not resulted in the discovery of greatly superior genotypes. The following procedure might yield improved forms: It should be possible to find an ascogenous heterothallic *Penicillium*

or *Aspergillus* with the ability to produce penicillin. Once this organism has been discovered its sexual mechanism can be exploited to produce different segregants, and those which are best from the point of view of penicillin production can be mated with each other, as well as with widely different forms. This method has been used successfully with yeasts (Lindegren & Lindegren 1945).

In *Neurospora* many, and probably most, of the isolates from nature are bisexual (heterokaryotic for both the A/a or +/- alleles) (Lindegren 1934) but sterility factors prevent copulation, so the mycelium appears to be unisexual. The most experienced observers may fail to detect such self-sterile bisexual heterokaryons. Lindegren (1936) has reported obtaining five cultures of *Neurospora* from Dr. B. O. Dodge, which were labelled Mexico A, Cuba A, Japan A, Japan B (= a), Panama B (= a). An elaborate series of experiments was required to show that all three of the A strains were bisexual, that is, they carried two kinds of nuclei (A and B, or A and a), but sterility factors prevented the production of perithecia.

Moreau and Moruzi (1931) performed experiments in which a culture of *Neurospora*, freshly isolated from nature, was planted in one side of a U-tube filled with agar, and a laboratory culture isolated from a single *Neurospora* ascospore (and therefore homokaryotic as far as sex is concerned) was planted in the other arm of the U-tube. Under such conditions the natural culture produced perithecia and ascospores. They proved conclusively that mycelium did not grow through the U-tube, so only the diffusion of some stimulating substance through the agar could account for the appearance of the perithecia. The culture which had been isolated from nature was incapable of producing perithecia except under these conditions. They concluded that this experiment proved that sex genes did not control the production of perithecia in *Neurospora*. Dodge (1932) and Aronescu (1934) criticized these experiments adversely, but Lindegren (1936) interpreted them as indicating that the culture which Moreau and Moruzi had isolated from nature was a bisexual, self-sterile heterokaryon which was made fertile by the diffusion of a substance from the homokaryotic culture. Lindegren (1934) suggested that self-sterile, bisexual heterokaryons occur frequently in nature among the filamentous ascomycetes because of their obvious high survival value. They enable the thallus to preempt a large area by virtue of its rapid vegetative growth but when vegetative growth has ceased the conidia can fertilize other thalli whether they be bisexual or unisexual. The practice of plating out *Penicillia* with their uninuclear conidia breaks up any heterokaryons which may be collected. In *Neurospora* the multinucleate conidia facilitate the maintenance of the heterokaryon.

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## CHROMOSOMES OF CRUCIFERAE—II. CYTOGEOGRAPHY OF *LEAVENWORTHIA*<sup>1</sup>

J. T. BALDWIN, JR.

Torrey (1837) established *Leavenworthia* with two species: *L. aurea* and *L. Michauxii*, and listed *Cardamine uniflora* Michx. as synonymous with the latter; Gray (1880), recognizing that the genus "has been almost from the first involved in some difficulty as to the species," added *L. torulosa* and *L. stylosa*; Britton (1894) made the combination *L. uniflora*. Svenson (1941) observed that "the species . . . are still obscure." Here, in the present paper, it is attempted by cytogeographic means to interpret the entities of the genus: there seem to be four rather well defined species—those designated by Torrey and by Gray.

The Nashville Basin of Tennessee is the center of generic variability: for discussion and delimitation of the Nashville Basin see Fenneman (1938, p. 431-434 and pl. 6). Representatives of the four species occur together there (see figures 6-9); e.g., a letter in the Gray Herbarium, under date of May 8, 1880, from A. Gattinger to Asa Gray, reads with reference to *Leavenworthia*: "I found this time . . . three species on one square yard of ground," near Nashville, Tennessee, and the specimen transmitted with that letter and from that spot is apparently of the fourth species, *L. aurea*. A balance of selective advantages among the species must exist. From that region the genus extends sporadically through Kentucky into Highland and Adams counties, Ohio, and into Clark County, Indiana, through much of Missouri into Kansas (*A. S. Hitchcock 31; Herbarium of Missouri Botanical Garden 213157*), through Arkansas to Choctaw County, Oklahoma, and as far south as San Augustine County, Texas, and Jefferson County, Alabama.<sup>2</sup> The plants are calciphilous winter-annuals: they characteristically grow on limestone.

Several years ago, with the help of a number of individuals—to whom appreciation is here expressed—the writer brought together twenty-seven living collections of *Leavenworthia* more or less representative of the geo-

<sup>1</sup> Contribution from the Department of Botany, University of Michigan, and from The Blandy Experimental Farm, University of Virginia.

<sup>2</sup> A specimen of *L. torulosa* of doubtful origin in Louisiana is in the Herbarium of the New York Botanical Garden, and one of indeterminate identity and questionable origin in Illinois is in the Herbarium of the Brooklyn Botanic Garden. In various herbaria are J. M. Coulter's specimens from Jefferson County, Indiana; it is explained in a letter of November 7, 1944, from C. C. Deam that those specimens were in all likelihood collected in Clark County. It is stated by F. C. Gates in a letter of October 31, 1944, that "while one might think that *Leavenworthia uniflora* might grow in Kansas, there is no evidence that I know of that it does, and no specimens in our state herbarium."

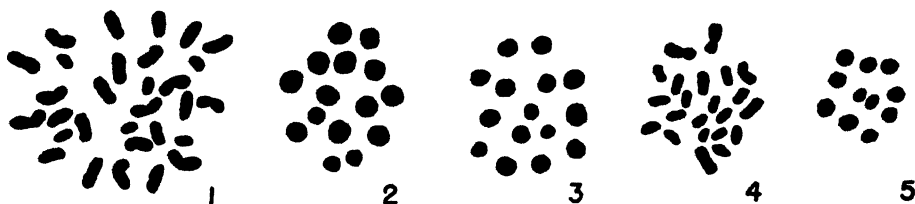
TABLE 1. *Collections of Leavenworthia for which chromosomes were counted.*

Species and source	n	2n	Collector	Author's number
<i>L. uniflora</i> (Michx.) Britton				
Missouri				
Franklin County: Gray Summit	30		Edgar Anderson	2550
Kentucky				
Caldwell County: Princeton	30		A. M. Harvill	2551, 2552
Simpson County: at Tennessee line	30		B, S & H <sup>a</sup>	2553, 2554
Tennessee				
Knox County: Mascot	30		A. J. Sharp	2555, 2556
Knox County: Hall's Crossroads	30		A. J. Sharp	2557, 2558, 2559
Wilson County: Lebanon	30		C. C. Deam	2560
Rutherford County: Murfreesboro	30		B, S & H	2561, 2562
Rutherford County: Murfreesboro	30		B, S & H	2563
Davidson County: Nashville	30		B, S & H	2564, 2565, 2566
<i>L. torulosa</i> Gray				
Tennessee				
Rutherford County: La Vergne	30		B, S & H	2567, 2568
Davidson County: Nashville	15	30	B, S & H	2569, 2570
Davidson County: Nashville	15	30	B, S & H	2571, 2572
Sumner County: Gallatin	30		C. C. Deam	2573, 2574
Brooklyn Botanic Garden	15	30	H. K. Svenson	
<i>L. stylosa</i> Gray				
Tennessee				
Wilson County: Lebanon	15	30	C. C. Deam	2575, 2576
(petals yellow)				
Wilson County: Cedar of Lebanon	15	30	C. C. Deam	2577, 2578
State Park				
(petals white or purple with yellow base)				
Wilson County: Lebanon	30		B, S & H	2579, 2580
(petals yellow or petals white or purple with yellow base)				
Wilson County: Lebanon	30		C. C. Deam	2581, 2582
(petals yellow)				
Rutherford County: La Vergne	15	30	L. M. Dickerson	2583, 2584, 2592
(petals yellow)				
Rutherford County: Murfreesboro	30		B, S & H	2585, 2586
(petals white with yellow base)				
Rutherford County: Murfreesboro	30		B, S & H	2587
(petals purple with yellow base)				
Davidson County: Nashville	30		A. J. Sharp	2588, 2589
(petals yellow)				
Davidson County: Nashville	30		A. J. Sharp	2590, 2591
(petals yellow)				
Davidson County: Nashville	15	30	B, S & H	2593, 2594
(petals yellow)				
Davidson County: Nashville	30		B, S & H	2595, 2596
(petals yellow)				
Brooklyn Botanic Garden	30		H. K. Svenson	
(petals purple with yellow base)				
<i>L. aurca</i> Torrey				
Tennessee				
Davidson County: Nashville	11	22	A. J. Sharp	2597, 2598

<sup>a</sup> J. T. Baldwin, Jr., H. T. Shacklette, and A. M. Harvill.

graphic range of the genus (table 1). The collections, with three exceptions, were grown from seed under uniform conditions in the University of Michigan Botanical Gardens. Certain plants of each species were isolated to determine the status of self-fertility for the species. The  $2n$ -number of chromosomes for each collection was established from aceto-carminic smears of leaves of young plants and from smears of roots of pot-bound plants; the  $n$ -number of chromosomes at microsporogenesis was ascertained for some of the collections. A comprehensive set of cytologically studied specimens of various ages has been placed in the University of Michigan Herbarium. Distribution maps for the four species are based upon specimens borrowed from eleven herbaria.<sup>3</sup> Many of the specimens were wrongly identified.

*L. uniflora* (Michx.) Britton is a clear-cut species and is seldom confused in the herbaria. Its leaves, in contrast to those of the other species, are finely



FIGS. 1-5. Chromosomes of *Leavenworthia*. FIGS. 1-3. *L. stylosa* Gray at mitotic metaphase and at first and second meiotic metaphase— $2n = 30$ ,  $n = 15$ . FIGS. 4, 5. *L. aurea* Torrey at mitotic metaphase and at first meiotic metaphase— $2n = 22$ ,  $n = 11$ . Note the six small chromosomes in *L. stylosa*. Magnification  $ca \times 2000$ .

dissected "with many small sharp-toothed or angulate segments." In the nine collections grown (table 1) the petals were white with a yellow claw; upon drying, the petals often become yellowish, which is the basis for Torrey's (1837) "opinion that the flowers . . . are pale yellow." Gray (1880) described the petals as "white with purplish tinge." The silique is non-torulose and linear with a short, and usually stout, style. The  $2n$ -chromosome number for the plants investigated was thirty. This species has by far the widest distribution, being absent, it would seem, from only the southern and southwestern parts of the generic range (fig. 6).

<sup>3</sup> The herbaria of the United States National Museum, Chicago Natural History Museum, United States National Arboretum, New York Botanical Garden, Brooklyn Botanic Garden, Missouri Botanical Garden, Gray Herbarium, University of Kentucky, University of Tennessee, University of Michigan, and C. C. Deam Herbarium. For their coöperation the writer is grateful to the curators of these herbaria: it was a privilege to examine the specimens. Among the material borrowed from the New York Botanical Garden were designated types of *L. aurea* Torrey collected by M. C. Leavenworth in Texas (or Oklahoma?) and of *L. Michauxii* collected by C. W. Short in Kentucky and isotypes of *L. stylosa* Gray collected by A. Gattinger in Tennessee and of *L. torulosa* Gray collected by C. W. Short in Kentucky; among that from the Gray Herbarium, a photograph of the type of *Cardamine uniflora* Michaux, collected by him near Knoxville, Tennessee, and deposited in the Herbarium du Muséum national d'histoire naturelle de Paris.

*L. torulosa* Gray is likewise usually distinct: leaves coarsely dissected, flowers light purple, fruit torulose and linear with prominent style. The species apparently intergrades somewhat with *L. stylosa*. The five collections investigated cytologically had  $2n = 30$ ,  $n = 15$  (table 1). The distribution area extends from Central Tennessee into Kentucky (fig. 7): occurrence of the species in Louisiana (see footnote 2) and at Allenton, Missouri, as



FIG. 6. Distribution of *Leavenworthia uniflora* (Michx.) Britton: big circles, specimens examined cytologically; little circles, specimens in herbaria.

evidenced by one plant of *L. torulosa* mixed on a sheet with *L. uniflora* (*Herbarium of the Missouri Botanical Garden* 774303), is questioned. Dr. C. W. Short's collections have indefinite citations of locality: "barrens of Kentucky" (type), "in the west of Kentucky," and "limestone cliffs of Kentucky river."

*L. stylosa* Gray is, with respect to flower and fruit, the most variable



species in the genus. It seems rather constant in foliage: leaves with relatively few angled or lobed segments. Thirteen collections were grown; the petals were yellow, or were white or purple (in differing intensity and pat-



FIG. 7. Distribution of *Leavenworthia torulosa* Gray: big circles, specimens examined cytologically; little circles, specimens in herbaria.

tern) with yellow base (table 1). Yellow is much the commonest color: it may be that entirely yellow petals occur in no other species of *Leavenworthia*.<sup>4</sup> The flowers of this species are big in comparison with those of

<sup>4</sup> Sharp (1940) would give varietal designation to a plant "with flowers identical in color with those of *Oxalis violacea*" (*R. E. Shanks & A. J. Sharp 386*: near Murfreesboro, Rutherford County, Tennessee); that seems not wise: such recognition requires comparable treatment for coordinate differences, of which there are others in this species; it appears far better in such cases merely to record variations rather than to use them for nomenclatorial notice with consequent systematic encumbrance. *R. M. Harper 3876* (near Isbell, Franklin County, Alabama) exhibits the same color pattern, as do a number of the specimens listed in table 1. The plant figured by Hooker (1868) has the same character and is referable here.

other representatives of the genus; the plant would make an attractive ornamental. The fruits are siliques with 3-6 seeds or many-seeded siliques to 25 mm. long and of variable width; styles are conspicuous and to a length of 6 mm. The chromosome number for twelve collections was  $2n = 30$ ,  $n = 15$  (figs. 1-3). The species has a restricted occurrence in Central Ten-



FIG. 8. Distribution of *Leavenworthia stylosa* Gray: big circles, specimens examined cytologically; little circles, specimens in herbaria.

nessee, in northwest Alabama (fig. 8), and in "Kentucky" (*Chicago Natural History Museum* 790163). Svenson's (1941) figure of *L. torulosa* belongs here.

Individuals of *L. stylosa* isolated in the greenhouses at the University of Michigan Botanical Gardens set few or no seed: the plants were highly self-sterile. Under the same conditions representatives of the other species were highly self-fertile. But when pots of *L. stylosa* were crowded together on the

greenhouse bench, the plants usually produced many seed: pollination between individuals probably occurred. In nature *Leavenworthia* generally grows in thick stands. It would be of significance to determine for a species that is highly self-sterile the relation between initial population size and the maintenance capacity: one would expect high positive correlation between the number of individuals and survival, and the same, of course, for a self-fertile group, but in less degree. Such differentials in survival have a direct bearing on the efficiency index of migration of species, and especially if one considers that often the entry of a species into a new locality is a matter of chance. If cross-pollination is obligate for *L. stylosa*, that might account for the instability and variation in the species: mutations would be assured trials in all combinations. The big and showy flowers suggest in this regard that the species is insect-pollinated, and differences in color frequencies might in some measure be explained thereby: East and Glaser (1914), for example, found in *Nicotiana* that certain insects effecting pollination showed marked preferences for given flower colors.

*L. aurea* Torrey has not infrequently been confused with *L. stylosa*. The type of *L. aurea*, from the Shortian Herbarium, was collected in Texas (or Oklahoma?) by M. C. Leavenworth, M.D., of the United States Army, and on his authority the label indicates that the plant has "flowers golden yellow." Thus the specific name. But it is altogether likely that the color was wrongly recorded, and the specific name, therefore, misleading. The only collection grown during the present study had white petals with yellow claws, and Small (1933) states that the petals are "white or purplish, except the yellow base"; this description seems to hold for the herbarium specimens examined by the writer, but colors cannot be determined with certainty from dried flowers. Gray (1880) noted that Alabama representatives of the species had "petals purple, pale rose, or white, with yellowish base, sometimes fully half inch long": he was not distinguishing between *L. aurea* and *L. stylosa*. *L. aurea* has leaves with relatively large, blunt-lobed segments, and in this resembles *L. stylosa* and *L. torulosa* and differs from *L. uniflora*. The silique is oblong-linear, non-torulose, and has a conspicuous style. The plants of the only collection studied cytologically had a chromosome number of  $2n = 22$  (fig. 4) and  $n = 11$  (fig. 5), which contrasts with the uniformity of  $2n = 30$ ,  $n = 15$ , as known for the rest of the genus. Distribution is given in figure 9. As now understood, the occurrence of the species is disjunct. It extends farther south than any other species. The herbarium specimens from Texas and Oklahoma seem more robust than the plants from Alabama and Tennessee.

Indications are that *Leavenworthia* is predominantly hexaploid. At mitotic metaphase in *L. stylosa* six chromosomes are smaller than the other twenty-four (fig. 1); at first meiotic metaphase three of the fifteen bivalents

are clearly small (fig. 2); at second meiotic metaphase three of the chromosomes are smaller than the others (fig. 3). Moreover, the condition of  $2n = 22$ ,  $n = 11$ , in *L. aurea* could well be interpreted as derived from a straight tetraploid of  $2n = 20$ ,  $n = 10$ . Additional survey of the genus might reveal the existence of such a race, as well as of a diploid of  $2n = 10$ ,  $n = 5$ ,



FIG. 9. Distribution of *Leavenworthia aurea* Torrey: big circles, specimens examined cytologically; little circles, specimens in herbaria.

but, on the other hand, if there were such races of *Leavenworthia*, they may have been evolutionarily inept and may no longer exist.

And what about interspecific relations? On the evidence at hand *L. aurea* appears to be the oldest species: it has the lowest chromosome number; it occurs farthest south, and, since the genus is part of a flora that apparently receded under glacial influence, this specific range has significant meaning, particularly since the range is not continuous. *L. stylosa* might be inter-

puted as the hexaploid phase of the same complex and as the second oldest species: it is often confused with *L. aurea*; it is highly self-sterile; it is a group in which the "trial of variations" is in progress; it is an entity most likely to produce other entities that are distinct. *L. uniflora* can be considered such a product and as the third oldest species: it too is hexaploid, but self-fertile and, even when isolated, productive of many seed; it, perhaps fortuitously as well as from the result of certain advantages, can be assumed to have entered new territory and, in large measure, to have preëmpted the ecological situations available to the genus. *L. torulosa* is, accordingly, to be regarded as the youngest species: it is hexaploid and highly self-fertile but restricted in range. In its foliage, habit of growth, its somewhat large flowers of purplish color, and its longish style, the species shows affinity to *L. stylosa*.

*L. torulosa* and *L. stylosa* are in great degree within the Nashville Basin, as delimited by Fenneman; *L. aurea* and *L. uniflora* extend out from there. The Nashville Basin is a part of the Interior Low Plateau. The latter is bounded by the Cumberland Plateau, by the upward extension of the Coastal Plain province from the Gulf of Mexico, and, on the north, by the Till Plain, "in which an older topography like that of the Interior Low Plateau is buried" (Fenneman 1938). The rocks are Ordovician—"generally bluish-gray, fossiliferous limestone, and calcareous shales of varying characters; phosphatic in many horizons; knotty, earthy, and unevenly bedded" (Pond). Much of the Basin consists of "glades," as the more or less flat areas of bare rock, or rocky places, with all gradations between the proportions of rock to soil, from perfectly bare rock to rocky fields which can be farmed, are designated in Tennessee (Galloway 1919). And glades are of two types: red-cedar glades on platy, thin-bedded Lebanon limestone, or rarely Pierce; hardwood glades, usually on Ridley limestone, with "flat areas of solid, bare rock with few cracks," or "areas of massive or chunk rock with numerous joints or vertical cracks partially filled with soil" (Galloway 1919). These glades have a characteristic flora, of which *Leavenworthia* is a typical element.

The only other representative of this flora that has been subjected to detailed cytogeographic analysis is *Sedum pulchellum* Michx. (Baldwin 1943). It too is a caespitilous winter annual. Its range is just about the counterpart of that of *Leavenworthia* (see distribution map in Baldwin 1943). It consists of diploid, tetraploid, and hexaploid races:  $2n = 22, 44, 66$ . The hexaploid race, as known, is restricted to the Nashville Basin; the other two races, with extensive ranges, are also represented there.<sup>5</sup>

<sup>5</sup> Baldwin (1943) postulated that diploid *S. pulchellum* ( $2n = 22$ ) might be the amphidiploid result of hybridization of a 5-chromosome line of evolution in *Sedum*—as now exemplified by *S. Nuttallianum* Raf. ( $2n = 20$ ), with a present range from south-

How does one account for the similarities between the evolution patterns of these two complexes, one of the Cruciferae, the other of the Crasulaceae? It seems logical to consider that both complexes once occurred, via diploid representatives, to the north of their present ranges and on the older formations now covered by the Till Plain, but, with glacial advance, they moved south—or were killed out to at least the approximate latitude of Nashville, and on both sides of the Mississippi River. Then, one concludes, tetraploidy was established in the Nashville Basin for *S. pulchellum*, and, with recession of the glacier, the species moved northward again, to the east of the Mississippi as a tetraploid, to the west as a diploid: its migration was checked by the Till Plain. And hexaploidy was doubtless effected in Tennessee where the diploid and tetraploid races met. The story of *Leavenworthia* is not quite so clear: the genus needs more cytogeographic study. It may be that both the diploid and straight tetraploid races were exterminated during one of the glacial periods. It is important in this regard that the representatives of *L. aurea* in Alabama and in Texas be investigated and with the not unreasonable expectation of discovering one, or both, of the “missing” races. But the races were probably in existence in Tennessee until hexaploidy became fixed (in *L. stylosa* ?); however, it is remembered that hexaploidy might evolve through doubled pollen as well as through diploid-tetraploid crossing, and it is assumed, for example, that hexaploid *S. ternatum* at the southern limit of the species and in association with the tetraploid race so arose (Baldwin 1942). Return northward of *Leavenworthia* on both sides of the Mississippi was through the medium of hexaploid *L. uniflora*: it reached the edge of the Till Plain. That the Nashville Basin is the center of variability for both *Leavenworthia* and *S. pulchellum* probably has an explanation in this: there, because of patchiness of the soil—which is of the type to which these plants are adapted—many separate populations, and of greatly varying sizes, become established; each year the plants, being annuals, died out; mutations and chromosomal changes occurred and became fixed either through adaptive differentiation by selection or through drift by accident, depending on population size; with the passage of time inter-population migrations took place—and the immigrant annual, as contrasted with perennials, has promise of a good future—and, as soil areas increased, populations merged: these would appear to rank high among the desiderata for rapid and effective evolution. Accidents of

western Missouri into Texas—with a 6-chromosome line, as now expressed in *S. Nevii* Gray ( $2n=12$ ), with occurrence in Alabama. Further, Baldwin (1944) suggested an amphidiploid origin of diploid *S. Beyrichianum* Masters ( $2n=28$ )—known to the writer in Virginia and West Virginia—through *S. Nevii* ( $2n=12$ ) and diploid *S. ternatum*, Michx. ( $2n=16$ ), which occurs in southern West Virginia, southwestern Virginia, and eastern Kentucky (Baldwin 1942). The ranges of these sedums were changed under influence of glaciation: the subject will be discussed in detail in a later paper on cytogeography and glaciation.

"ploidy" for these plants were probably not restricted to the Nashville Basin, but, for topographic reasons, such happenings had there better chance of permanent modification of the complex. Intensive study of other elements in the flora of the glades will probably turn up parallels to the basic patterns exhibited by *Leavenworthia* and *S. pulchellum*.

#### SUMMARY

*Leavenworthia* seems to consist of four rather well-defined species, of which the geographic ranges and characteristics are given. Three of the species are considered to be hexaploid:  $2n = 30$ ,  $n = 15$ , and the fourth, *L. aurea*, an aneuploid derivative from tetraploidy:  $2n = 22$ ,  $n = 11$ . *L. uniflora* is the most clear-cut species and has the greatest distributional area. *L. stylosa* is the most variable species, a condition probably correlated with its self-sterility as contrasted with a high degree of self-fertility in the others, and it has large and showy flowers. *L. torulosa* has the most limited range; it is probably the youngest species and perhaps intergrades somewhat with *L. stylosa*, which, however, is more often confused with *L. aurea*. Because of its southernmost occurrence, disjunct range, and lower chromosome number, *L. aurea* appears to be the oldest member of the genus, and it possibly harbors diploid and tetraploid races: its representatives in Texas have a different aspect from those in Alabama and Tennessee.

The center of variability for *Leavenworthia* is in the Nashville Basin, where all the species occur and to which two of them are in large measure restricted. The genus is one of the characteristic elements of the "glade" flora. The only other complex of the flora that has been studied in cytogeographic detail is *Sedum pulchellum*, with diploid, tetraploid, and hexaploid races: the range of the species and the center of its variability are almost the counterparts of those of *Leavenworthia*. It is suggested that the basic pattern expressed by these complexes—one of the Cruciferae, the other of the Crassulaceae—is a reflection of glacial influence and of the topography of the Nashville Basin, which since mid-Pleistocene has been favorable for the establishment of many populations of varying sizes within which both adaptive differentiation and drift might operate effectively and, because of the annuality of the plants, at a rapid rate. It is expected that other elements of the glade flora have comparable patterns of evolution.

THE BLANDY EXPERIMENTAL FARM  
BOYCE, VIRGINIA

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**JUNIPERUS VIRGINIANA, J. HORIZONTALIS AND J. SCOPULORUM—IV. HYBRID SWARMS OF J. VIRGINIANA AND J. HORIZONTALIS**

NORMAN C. FASSETT

*J. virginiana* ranges northwestward to southern Maine, northern New York, southern Ontario, northwestern Wisconsin, southern Minnesota, and southwestern North Dakota, while the more northern and local *J. horizontalis* overlaps this range in a few regions; two of these regions have been studied in detail. Except in these regions of overlap, the two species are quite distinct on several characters,<sup>1</sup> of which the four most conveniently dealt with are: (1) the epidermal cells of the leaves of *J. virginiana* average 9–12  $\mu$  in width, those of *J. horizontalis* 13–19  $\mu$ ; (2) the leaf-tips of *J. virginiana* are rarely apiculate, those of *J. horizontalis* always apiculate; (3) *J. virginiana* is an erect tree, *J. horizontalis* a creeping shrub, and (4) in *J. virginiana* not more than a third of the peduncles of the female cones are curved, and in *J. horizontalis* half or more are curved.

TABLE 1. Twelve individuals of *Juniperus* from Grand Marsh, Wisconsin

Average width of epidermal cells, in micra	Habit	Leaf-tips	Per cent peduncles curved	Identity
10.0	Erect	Acute	.	<i>virginiana</i>
10.0	Erect	Acute	.	<i>virginiana</i>
10.2	Erect	Acute	.	<i>virginiana</i>
12.2	Erect	Acute	.	<i>virginiana</i>
12.7	Erect	Acute	.	<i>virginiana</i>
13.0	Creeping	Apiculate	78	<i>horizontalis</i>
13.2	Creeping	Apiculate	.	<i>horizontalis</i>
14.2	Creeping	Apiculate	.	<i>horizontalis</i>
15.0	Creeping	Apiculate	.	<i>horizontalis</i>
16.0	Creeping	Acute	.	<i>horizontalis</i>
17.6	Creeping	Apiculate	82	<i>horizontalis</i>
18.0	Creeping	Apiculate	.	<i>horizontalis</i>

On the coast of Maine, and in the Driftless Area of Wisconsin, where the two species overlap in range, a sample has been taken from each individual in a colony,<sup>2</sup> and the character of each individual recorded in tables 1–6.

At Grand Marsh, Wisconsin (Sect. 31, T. 16 N., R. 7 E.), a colony of *Juniperus* on a hillside and sandstone cliffs consists of a number of erect trees and many creeping shrubs. Close examination of the characters of each shows (table 1) the erect trees to be pure *J. virginiana* and the creeping

<sup>1</sup> See Fassett, Bull. Torrey Club 71: 410–418. 1944.

<sup>2</sup> Much of the necessary travel in this study was financed by the Wisconsin Alumni Research Foundation.

shrubs to be pure (or almost pure) *J. horizontalis*. At this station, then, the two species grow together with little or no interchange of characters. There appear to be internal barriers between the two species.

About a mile east of New Glarus, and conspicuous across the valley from the north side of the town, is a cedar-covered hillside. Only two of the plants are erect (table 2) and these prove to be good *J. virginiana*. The rest of the plants are creeping, looking exactly like *J. horizontalis*, but of these only a few prove to have the other characters of that species. One is *J. horizontalis* in all except its non-apiculate leaf-tips. The rest of the creeping shrubs have epidermal cells of leaves averaging less than 13  $\mu$  in width, and leaf-tips not

TABLE 2. *Eighteen individuals of Juniperus from New Glarus, Wisconsin*

Average width of epidermal cells, in micra	Habit	Leaf-tips	Per cent peduncles curved	Identity
9.7	Erect	Apiculate		<i>virginiana</i>
10.0	Creeping	Apiculate		<i>v. ambigens</i>
10.8	Creeping	(Juvenile)		<i>v. ambigens</i>
11.2	Creeping	(Juvenile)		<i>v. ambigens</i>
11.5	Erect	Subapiculate		<i>virginiana</i>
12.3	Creeping	Subapiculate		<i>v. ambigens</i>
12.3	Creeping	Acute		<i>v. ambigens</i>
12.7	Creeping	Apiculate		<i>v. ambigens</i>
13.5	Creeping	Apiculate		<i>horizontalis</i>
13.8	Creeping	Apiculate		<i>horizontalis</i>
14.3	Creeping	Apiculate		<i>horizontalis</i>
15.0	Creeping	Apiculate		<i>horizontalis</i>
15.3	Creeping	Apiculate		<i>horizontalis</i>
15.3	Creeping	Subapiculate		<i>horizontalis</i>
15.7	Creeping	Subapiculate		<i>horizontalis</i>
15.8	Creeping	Acute		<i>horizontalis</i>
17.5	Creeping	Apiculate		<i>horizontalis</i>
18.2	Creeping	Apiculate		<i>horizontalis</i>

apiculate. At this location none were found fruiting, but similar plants at other places have a great majority of the peduncles straight.

These plants, combining the foliage and fruit of *J. virginiana* with the habit of *J. horizontalis*, are a definite and easily recognized element of the *Juniperus* population in several places where the ranges of the two (presumably parent) species overlap. Of course, its hybrid origin is by no means demonstrated. For convenience, these plants may be called:

*J. VIRGINIANA* L., var. **ambigens** Fassett, var. nov., caulibus humilis, repentibus vel subascendentibus; foliis pleurumque non apiculatis, epidermidis cellulis latis 5–20 mm., pleurumque 10 mm.; pedicellis pleurumque rectis. MAINE: Needles Eye Island, Thread-of-Life Ledges, Bristol, August 6, 1941, *Fassett 22125* (TYPE in Herb., Univ. of Wis.); exposed sea-cliffs, Small Point, August 4, 1930, *Fassett 10392*; Ogunquit, September 27, 1925, *W. H. Judd* (this and the following collections from Maine are in the Arnold Arboretum); Western Brown Cow, Casco Bay, August 15, 1908, *Norton &*

*Chamberlain 1111*; Bald Head Cliff, August 9, 1929, *Susan D. McKelvey 3*. WISCONSIN: Sandstone Knob, Prairie du Sac, April 11, 1932, *Fassett 13680* (one trunk erect, with branches trailing); dry crumbling sandstone bluffs, Primrose Twp., Dane County, June 17, 1926, *Fassett 2719*;<sup>3</sup> crumbling sandstone bluff, south of Dane County line, near Belleville, May 26, 1929, *Fassett 8366*.

Several horticultural varieties of *J. virginiana* have been described as low or dwarf forms, but these seem to have no relation to native populations.

At Pine Bluff, Wisconsin, 15 miles west of Madison, a sandstone hillside is covered with cedars, which by their variety of forms present a puzzling aspect. There are erect trees, obviously typical *J. virginiana*; there are

TABLE 3. *Thirteen individuals of Juniperus from Pine Bluff, Wisconsin*

Average width of epidermal cells, in miera	Habit	Leaf-tips	Per cent peduncles curved	Identity
10.0	Erect	Acute		<i>virginiana</i>
10.3	Creeping	Acute	0	<i>v. ambigens</i>
10.5	Erect	Acute		<i>virginiana</i>
10.7	Creeping	Apiculate	11	<i>v. ambigens</i>
10.8	Ascending	Acute		<i>v. ambigens</i>
11.0	Ascending	Acute		<i>v. ambigens</i>
11.5	Creeping	Acute		<i>v. ambigens</i>
11.7	Ascending	Apiculate		<i>v. ambigens</i>
11.7	Erect	Subapiculate	9	<i>virginiana</i>
12.2	Creeping	Acute		<i>v. ambigens</i>
13.3	Creeping	Apiculate		<i>horizontalis</i>
13.5	Creeping	Apiculate	42	<i>horizontalis</i>
14.5	Part creeping, part ascending	Acute	33	

creeping shrubs, apparently *J. horizontalis*; and with these extremes occur plants with the matted habit and ascending branches of *J. communis* var. *depressa*, some scarcely half a meter in height, others ranging to 2 meters; in a few cases an erect tree has branches which trail out almost enough to simulate *J. horizontalis*. This colony is analyzed in table 3; *J. virginiana* and *J. horizontalis* prove to be present, *J. virginiana* var. *ambigens* is present in its extreme creeping form and grades into a type with somewhat ascending branches.

From its generally disrupted range, we may hypothesize that *J. horizontalis* survived the most recent glaciation in the Driftless Area, and that in post-Wisconsin times *J. virginiana* has migrated into the area from the south. When the two species have met, they have sometimes remained dis-

<sup>3</sup> Some of these collections may be different in different herbaria, since they were collected without a knowledge of the variation in this group and may represent different individuals.

TABLE 4. *Ten individuals of Juniperus from Bald Head Cliff, Maine*

Average width of epidermal cells, in micra	Habit	Leaf-tips	Per cent peduncles curved	Identity
9.5	Ascending	Acute	....	<i>v. ambigens</i>
9.8	Creeping	Subapiculate	....	<i>v. ambigens</i>
10.2	Creeping	Acute	12	<i>v. ambigens</i>
10.3	Ascending	Acute	10	<i>v. ambigens</i>
10.8	Ascending	Subapiculate	....	<i>v. ambigens</i>
12.0	Creeping	Subapiculate	59	.....
12.3	Erect	Acute	..	<i>virginiana</i>
13.0	Ascending	Subapiculate	51	.....
13.0	Ascending	Apiculate	24	.....
15.5	Ascending	Subapiculate	....	.....

tinet (as at Grand Marsh), and sometimes produced a series of hybrids, which may fall into a fairly uniform type (as at New Glarus), or may result in a more or less blending series from one species to the other (as at Pine Bluff). On the coast of Maine, on the other hand, study of colonies from York County to Monhegan Island shows a gradation from a preponderance of *virginiana* characters to one of *horizontalis* characters.

The cedars along the coast of York County, Maine, have been collected by many botanists, with resulting specimens in herbaria labeled "*J. virginiana prostrata*," "*J. horizontalis*" and annotated "*J. virginiana*," "*J. Sabina procumbens?*," "*J. virginiana*, var.," "*J. virginiana* var. *reptans*," "*J. virginiana horizontalis*," "*J. virginiana* var. *Kastenii*," etc.

The colony at Bald Head Cliff has been analyzed (table 4) and shows plants with various combinations of the characters of *J. virginiana* and *J. horizontalis*. While most of the individuals can be fitted into one species or the other, or into *J. virginiana* var. *ambigens*, the last three in table 4

TABLE 5. *Thirteen individuals of Juniperus from Thread-of-Life Ledges, south of Christmas Cove, Maine*

Average width of epidermal cells, in micra	Habit	Leaf-tips	Per cent peduncles curved	Identity
10.0	Creeping	Apiculate	..	<i>v. ambigens</i>
10.7	Creeping	Acute	37	<i>v. ambigens</i>
11.5	Creeping	Acute	34	<i>v. ambigens</i>
12.4	Creeping	Apiculate	....	<i>v. ambigens</i>
12.5	Creeping	Apiculate	....	<i>v. ambigens</i>
13.0	Creeping	Apiculate	....	<i>horizontalis</i>
13.0	Creeping	Apiculate	25	<i>horizontalis</i>
14.0	Creeping	Acute	35	<i>horizontalis</i>
14.5	Creeping	Apiculate	....	<i>horizontalis</i>
14.5	Creeping	Apiculate	15	<i>horizontalis</i>
15.0	Creeping	Acute	27	<i>horizontalis</i>
15.0	Creeping	Acute	52	<i>horizontalis</i>
15.5	Creeping	Acute	....	<i>horizontalis</i>

seem to have the foliage of *J. horizontalis* with an admixture of *J. virginiana* shown by a suberect habit; this combination seems much less common than is that of *virginiana* foliage with *horizontalis* habit. Another tree in table 4 would be *J. virginiana* var. *ambigens*, but has 59 per cent of the peduncles curved.

About 70 miles "down" the coast, on the ledges extending southward from Christmas Cove, Lincoln Co., the rocks are covered with creeping cedars, all of which would, on sight, be pronounced *J. horizontalis*. But a close study of their characters (table 5) shows that nearly half of these shrubs have the foliage of *J. virginiana*. On the basis of the width of epider-

TABLE 6. *Eleven individuals of Juniperus from Monhegan Island, Maine*

Average width of epidermal cells, in micra	Habit	Leaf-tips	Per cent peduncles curved	Identity
14.3	Creeping	Apiculate	75	<i>horizontalis</i>
14.3	Creeping	Apiculate	90	<i>horizontalis</i>
14.7	Creeping	Subapiculate	85	<i>horizontalis</i>
14.7	Creeping	Apiculate		<i>horizontalis</i>
15.2	Creeping	Acute	92	<i>horizontalis</i>
15.5	Creeping	Apiculate		<i>horizontalis</i>
16.0	Creeping	Apiculate	83	<i>horizontalis</i>
16.0	Creeping	Apiculate	36	<i>horizontalis</i>
16.5	Creeping	Apiculate	90	<i>horizontalis</i>
16.8	Creeping	Apiculate	87	<i>horizontalis</i>
17.2	Creeping	Apiculate	82	<i>horizontalis</i>

mal cells all the individuals in this colony can be placed either in *J. horizontalis* or *J. virginiana* var. *ambigens*, but actually the leaf-tip characters and percentages of hooked peduncles do not correlate very well with other characters; i.e., the *virginiana* and *horizontalis* characters are somewhat mixed up together.

On Monhegan Island (table 6) the population seems to be fairly pure *J. horizontalis*, with only a slight possible indication of influence of *J. virginiana* in the one individual with leaf-tips not apiculate and one with peduncles only 36 per cent hooked.

#### SUMMARY

*Juniperus virginiana* and *J. horizontalis* show no intergradation except where their ranges overlap. In the Driftless Area of Wisconsin, the two species grow together, and in the same colony there may or may not be various intermediates. The most common intermediate, described as *J. virginiana* var. *ambigens*, combines the habit of *J. horizontalis* with the foliage and fruit of *J. virginiana*. On the coast of Maine, colonies nearer the range of *J. horizontalis* consist of individuals which are all creeping but which

often show some characters of *J. virginiana*. Colonies nearer the range of *J. virginiana* show all degrees from creeping to erect plants, with other characters of the two species occurring with little or no correlation of specific characters.

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## ON BLAKEA AND TOPOBEA

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No group of American melastomes is more easily recognized than the tribe Blakeae, characterized primarily by their axillary flowers each subtended closely by two pairs of decussate bracts, and secondarily by their usually 6-merous flowers with connivent anthers. They may be trees, lianas, or epiphytic trees; they sometimes cover the supporting tree so densely that they cause its death. Markgraf described one species as "frutex scandens suffocator"; in his notes on another he wrote "Das gesammelte Exemplar war 20 m. lang, sein Stützbaum bereits tot."

*Blakea* and *Topobea* are the two genera of the tribe. In *Blakea* the anthers are very stout, with a prominent connective often prolonged at base into a short conic spur. In *Topobea* the anthers are elongate and narrowly linear, the connective is scarcely thickened, and at base may be prolonged into a short delicate spur. No other character for the separation of the genera is known. Macbride recommends their union into one, and not without reason. Just as many botanists regret the unnecessary segregation of genera with the resulting confusion in literature, so do I regret any tendency to the unnecessary aggregation of genera, especially those which have a long botanical history, are well established in literature, and are capable of exact separation.

Since the genera can be distinguished only when flowers or large flower-buds are available, there has been abundant opportunity to refer herbarium specimens to the wrong genus and, after this preliminary error, to attach erroneous specific names to them or to describe them as "new" species.

The genus *Blakea* dates back to 1756 and the first binomial in the genus was published by Linnaeus for a Jamaican plant. *Topobea* was described by Aublet in 1775 and based on the single species of French Guiana. While a few other species of *Blakea* occur in the West Indies and became known at an early date, most of its species and almost all those of *Topobea* are Amazonian and Andean and were not discovered until comparatively recent times. A century ago eight species were known in both genera; Naudin, having access to collections by Funck & Schlim, Goudot, and Linden, increased the number to seventeen. Triana, largely on the basis of his own collections in the Andes and along the Pacific coast of Colombia, brought the total to 34 by 1871. Cogniaux recognized 55 in 1891, while recent collections in South and Central America have resulted in the description of 33 species of *Blakea* and twelve of *Topobea*, bringing the total to an even hundred. Doubtless some of these names are synonyms; Macbride has made a beginning in the

elimination of superfluous names by calling attention to several in his Flora of Peru.

Notwithstanding the great increase in described species in the last half century there still appear to be many others still unknown to the botanist. Nearly every collecting expedition into the region extending along the Cordilleras from Guatemala to Peru brings back plants which can not be referred to any known species. These always present a serious problem to the taxonomist who approaches his work thoughtfully. A species, in the current opinion of practical taxonomists, is a population of individuals, all much alike in many morphological features but also showing a reasonable degree of variability. In the study of species of the United States, field experience is easily obtained and our herbaria possess such large series that the general range of variability is evident. The species of *Topobea* and *Blakea*, growing in such inaccessible regions, are poorly known in the field and no herbarium has sufficient quantities of material to indicate the variations which may be expected in any one species. Shall we then describe as new those recent collections which can not be referred to known species, or shall we stretch characters inordinately and recognize only a few species of great morphological diversity?

As a general rule, taxonomists tend to follow the former course. Species therefore accumulate until finally the genus is studied comprehensively and necessary reductions are made.

Nevertheless, certain discoveries indicate that more valid species exist than the 55 recognized by Cogniaux. For example, *B. bracteata*, which I described in 1932, represented an entirely new type of structure for the genus, and was followed by the description of two or three more of the same general type from the rain-forests of upper Amazonia. My *B. calycosa*, with foliaceous appendages on the sepals, and my *B. glandulosa*, with glandular pubescence, also represent entirely new types.

There has been only one attempt, that of Cogniaux in 1891, to provide a key to all the known species and this proves to be largely artificial, species which are obviously much alike often being widely separated on some trivial distinction. Macbride provided two keys for the Peruvian species, which form a small minority of the total, and these are also obviously artificial.

The coastal forests of western Colombia and the adjacent slopes of the Cordillera Occidental have more species of the two genera than any other region and may well be regarded as their center of distribution. Among the recent collections of Dr. Cuatrecasas in western Colombia is a remarkably fine series of these interesting and often beautiful plants, mostly in full bloom so that they can be assigned to the proper genus. These form the basis of the remarks which follow. Cited collections are in the Britton Herbarium of the New York Botanical Garden.



**BLAKEA ANDREANA** Cogn. Although the outer bracts of this species are united to the middle, as shown by the type and clearly stated in the original description, Cogniaux placed it in the section *Eublakea*, characterized by bracts free or "rarius connatis." It seems closely related to *B. intercepta* and *B. brunnea*, which I have recently described from Costa Rica, and also to two undescribed species of Colombia. All have exceptionally large flowers with large coriaceous bracts nearly or quite as long as the obscurely lobed or truncate calyx. The Colombian species may be distinguished as follows:

Outer bracts free, ovate, acuminate ..... *B. clusiifolia*.  
Outer bracts connate at base, rotund.

Leaves elliptic, abruptly acuminate, furfuraceous on the primary veins  
beneath; plants of the Cordillera Oriental ..... *B. Andreana*.  
Leaves obovate, broadly rounded to a short apiculum, glabrous beneath;  
plants of the Cordillera Occidental ..... *B. Cuatrecasii*.

**Blakea clusiifolia** Gleason, sp. nov. Arbor 6–9 m. alta ubique glabra, ramis subteretibus. Petioli validi, 1–2 cm. longi; laminae subcoriaceae carnosae obovatae, usque ad 13 cm. longae 8 cm. latae, apice late rotundatae vel subretusae ad cuspidem linearem 5–8 mm. longam, integrae, basi cuneatae, 3-nerviae vel sub-3-pli-nerviae, jugo marginali neglecto, venis secundariis obscuris ca. 1.5 mm. distantibus, sub angulo ca. 70° adscendentibus. Pedunculi solitarii, 2.5 cm. longi, ad apicem valde incrassati. Bractee exteriores late ovatae, 25 mm. longae, acuminatae, quam interioribus obtusis duplo longiores. Flores ignoti.

TYPE: *Killip & Smith 15295*, from Mesa de los Santos, Dept. Santander, Colombia, alt. 1500 m.

**BLAKEA ANDREANA** Cogn. Known to me by the type collection of André, by *Killip & Smith 20197*, from Dept. Norte de Santander, alt. 2100–2400 m., and by *Laurance 153*, from Dept. Boyaca, alt. 2300 m.

**Blakea Cuatrecasii** Gleason, sp. nov. Arbor epiphytica glabra, ramis subteretibus. Petioli validi, 8–12 mm. longi. Laminae subcoriaceae carnosae, obovatae, superne late rotundatae ad cuspidem triangularem 3 mm. longam, integrae, basi cuneatae, trinerviae, jugo marginali neglecto, venis secundariis obscuris, sub angulo ca. 75° adscendentibus. Pedunculi solitarii validi suberecti, usque ad 4 cm. longi. Bractee exteriores coriaceae, 2.5 mm. connatae, rotundae, 18 mm. longae lataeque; interiores oblatae, coriaceae, 15 mm. longae, 19 mm. latae. Hypanthium coriaceum, hemisphaericum, ad oram 15 mm. latum. Calyx patulus integer 5 mm. latus. Petala obliqua obovata, alba venis roseis, 35 mm. longa 20 mm. lata. Filamenta 12.5 mm. longa. Antherae ovoideae, 11 mm. longae, medio ad filamentum affixae, poris 2 terminalibus dehiscentes; connectivum alte elevatum in carinam dorsalem, ecalcaratum. Stylus columnaris 12 mm. longus; stigma punctiforme.

TYPE: *Cuatrecasas 15180*, from the Cordillera Occidental, Dept. del Valle, alt. 900–1180 m. His number *14946*, from the same locality, is identical, except the petals are described as red ("rojos"). I can detect no differences of taxonomic importance in his numbers *16393* and *16638*, although they were collected at an altitude of only 5–50 m.; the petals of the former are described as "rojos exteriormente, rosado claros interiormente," those

of the latter as "blanco rosados." I also refer to this species *Killip 7914*, from the Micay Valley, Dept. El Cauca, alt. 1800–1900 m., originally reported as *B. Pyridanthus* Triana.

**Blakea calyptrata** Gleason, sp. nov. Arbuscula epiphytica, ramis teretibus tomentosulis. Petioli validi, 3–5 cm. longi, tomentosuli. Laminae subcoriaceae, ellipticae, usque ad 18 cm. longae 11 cm. latae, abrupte et breviter apiculatae, integrae, basi cuneatae vel obtusae, 5-plinerviae jugo marginali neglecto, supra glabrae subnitentes, subtus cinereo-stellato-tomentosae; venae secundariae 3–5 mm. distantes, sub angulo 80° adscendentes. Flores 2–5 axillares; pedunculi validi, superne incrassati, 1–2 cm. longi, dense tomentosi. Bracteae conformes distinctae, spathulatae, ca. 17 mm. longae, revolutae, tomentosae. Calyx calyptriformis, conico-ovoidens, ad torum circumscissilis, cum hypanthio cinereo-tomentosus, 5 mm. altus. Petala roseo-rubra, ut videtur obovata, certe 2 cm. longa. Filamenta ca. 5 mm. longa. Antherae ovatae, 6 mm. longae, poris binis terminalibus dehiscentes; connectivum in carinam angustam elevatum, basi infra thecas 2 mm. productum.

TYPE: *Cuatrecasas 14945*, collected in woods at Piedra de Moler, Dept. del Valle, alt. 900–1180 m.; *Cuatrecasas 15535*, from the same general region, is the same; also collected by Lehmann at Mesopotamia in Dept. Antioquia. A calyptriform calyx is hitherto unknown in the genus and the spatulate bracts are equally unexpected. There is no doubt that the plant belongs to the genus *Blakea*; in fact, the Lehmann collection was given a manuscript name in this genus by Cogniaux years ago.

In *Cuatrecasas 17524* we find the same calyptriform calyx, as indicated in its flowering condition by the truncate calyx. It agrees with the plants described above except in some minor matters of dimensions which are well within the limits of expected variability, and in its bracts. These are so different from those of the type that I propose a new variety:

**BLAKEA CALYPTRATA** var. **latior** Gleason, var. nov. Bracteae exteriores ovato-lanceolatae 8.3 mm. longae, 4.3 mm. latae, interiores rotundae, ca. 8 mm. longae lataeque.

TYPE: *Cuatrecasas 17524*, from the Pacific coast of Dept. del Valle, 5–80 m. alt.

**BLAKEA PODAGRICA** Triana. *Cuatrecasas 14420*, western slope of the Cordillera Occidental, alt. 350–450 m.; *16530*, *14315*, *16893*, *16992*, *17583* from the Choco Region. Bracts pale, herbaceous, conspicuously veined, ovate or ovate-lanceolate, up to 2 cm. long and much exceeding the cup-shaped hypanthium; sepals reflexed, triangular, acuminate. Every plant shows several of the upper internodes clavately thickened into formicaria.

**BLAKEA SUBCONNATA** Berg is known to me only from Ecuador. It is characterized by large, separate, herbaceous, acuminate bracts, and by the singular anastomose venation of the calyx-tube, a character not readily observed except by transmitted light. The petioles are conspicuously winged with the sides turned up, forming a deep channel. Two specimens from Colombia agree with these features, except that the bracts are round-ovate and very obtuse; they may be segregated as a variety:

**BLAKEA SUBCONNATA** var. **obtusa** Gleason, var. nov. Bracteae late rotundato-ovatae, obtusae.

TYPE: *Cuatrecasas 15644*, collected on the western slope of the Cordillera Occidental, Dept. del Valle, alt. 1400 m.; *Cuatrecasas 14988*, from the same region, is identical. His 17576 is obviously also the same, although collected at an altitude of 5–80 m.

**Blakea venosa** Gleason, sp. nov. Liana magna, ramis juvenilibus subteretibus sordide furfuraceo-tomentosis, pilis partim brevibus substellatis partim elongatis barbellatis. Petioli 1–2 cm. longi, graciles, non alati, supra canaliculati, furfuracei. Laminae tenues, elliptico-oblongae vel paullo obovatae, usque ad 12 cm. longae 6.5 cm. latae, superne abrupte rotundatae ad apiculum triangularem 5–8 mm. longum, basi late cuneatae vel obtusae, 5-plinerviae jugo marginali neglecto, supra glabrae subnitentes, subtus ad paginam glabrae ad venas sparse furfuraceo-pubescentes; venae secundariae fere horizontales 1 mm. distantes. Pedunculi solitarii vel bini, 1–2 cm. longi, dense ferrugineo-tomentosi, pilis barbellatis. Bractee exteriores ellipticae, ca. 22 mm. longae 19 mm. latae, distinctae, herbaceae, obtusae, minute apiculatae, multivenulosae, primo basi tenuiter furfuraceae at sparse strigosae, mox glabrescentes; interiores rotundae, ca. 22 mm. longae 25 mm. latae, glabrae. Hypanthium carnosum, hemisphaericum, glabrum, 6 mm. longum, ad oram 12 mm. latum. Calycis tubus patens, tenuis, 1.8 mm. latus; sepala ca. 5 mm. longa, late triangularia, venis reticulatis percurta, vena media in carinam angustam elevata. Petala rosea, obovata, 22 mm. longa. Antherae oblongae, 6 mm. longae, ut videtur ecalcaratae. Ovarium summo truncato-conicum, minute dentatum. Stylus 12 mm. longus; stigma punctiforme.

TYPE: *Cuatrecasas 14171*, collected at Guayabal on the Pacific coast, Dept. Cauca, alt. 5–20 m. The large herbaceous bracts completely concealing the calyx and the strongly anastomosing veins of the sepals show its close relationship to *B. subconnata*, from which it is distinguished by the pubescent stems, petioles, and peduncles, and the wingless petioles. Flowers are dissected with difficulty, as in *B. subconnata*.

**Blakea paleacea** Gleason, sp. nov. Petioli certe 8 cm. longi, subglabri. Lamina crassa subcoriacea late ovato-cordata 44 cm. longa 37 cm. lata, apice obtusa, apiculo lineari 2 cm. longo, basi late cordata, supra glabra, subtus ad paginam glabra opaca, ad venas primarias paleacea. Inflorescentia congesta 10–20-flora; pedunculi densissime paleacei usque ad 4 cm. longi. Bractee distinctae herbaceae multinerviae, exteriores ovato-lanceolatae 23 mm. longae, longe acuminatae, apicem versus ad costam dense paleaceae; interiores ovatae 18 mm. longae, ad apicem rugosae. Hypanthium cum calyce molliter carnosum glabrum 6 mm. longum; sepala late triangularia 3 mm. lata 0.7 mm. longa, venis anastomosantibus notata. Stamina immatura *Blakeae*.

TYPE: *Cuatrecasas 17271*, collected at Quebrada de Ordóñez, on the Pacific coast of El Valle, alt. 5 m. Its relation to *B. subconnata* is shown by its general habit, its sepals with anastomosing veins, and the general characters of its bracts; like that species it becomes very soft after boiling and dissection is difficult. It differs from both in its huge cordate leaves, its greatly elongate bracts, and its pubescence, which consists of stout flattened scales up to 2 mm. long which quickly break up into a mass of fibers. The collector's notes read "Varas 1 m. Cáliz verdoso amarillento. Corola roja."

**Blakea platypoda** Gleason, sp. nov. Arbor glabra, ramis ultimis crassis subteretibus. Petioli validi 2.5–4 cm. lati, late alati usque 2 cm. lati. Laminae subcoriaceae nitentes obovato-oblongae, usque ad 22 cm. longae 11 cm. latae, superne obtusae ad apiculum triangularem 8 mm. longum, basi obtusae, 3-nerviae jugo marginali neglecto; venae secundariae obscurae, 1.5 mm. distantes, sub angulo ca. 80° adscendentes. Pedunculi 1–3 in quaque axilla, usque ad 4 cm. longi. Bracteae subherbaceae distinctae subrotundae concavae, 20–22 mm. longae lataeque, obtusae, exteriores breviter apiculatae. Hypanthium hemisphaericum 7.5 mm. longum 12-costatum. Calycis tubus 3 mm. latus; sepala late rotundata e sinibus rotundatis, 1 mm. longa, venis anastomosantibus percursa, dente exteriori brevi subapicali notata. Stamina (jam immatura) *Blakeae*; antherae jam 8 mm. longae, ut videtur ecalcarata. Ovarium summo non productum.

TYPE: *Cuatrecasas 17027*, collected at Barco, on the Pacific coast of El Valle, alt. 5–80 m. This is a fourth member of the *subconnata* species group, as evidenced by the enlarged petioles, spurless anthers, veiny sepals, general habit, and the peculiar difficulty of dissection. *Cuatrecasas 17266E* is identical and has larger leaves up to 23 by 16.5 cm. The four species may be distinguished as follows:

Pubescence none, or obscure and furfuraceous.

Bracts short-acuminate to obtuse; leaves thin, opaque; petioles up to 1 cm. wide ..... *B. subconnata*.

Bracts obtuse or shortly apiculate, subcoriaceous; leaves firm, shining; petioles up to 2 cm. wide ..... *B. platypoda*.

Pubescence abundant, of long barbellate or fissile hairs.

Leaves obovate-oblong, 5-plexi-nerved; bracts elliptic, obtuse ..... *B. venosa*.

Leaves broadly cordate, 9-nerved; bracts ovate to lanceolate, long-acuminate ..... *B. paleacea*.

*Topobea alternifolia* was described by me in 1925, based on a specimen which showed foliage, bracts, and sepals, but not petals or stamens. It was collected again by Killip & Garcia, no. 33415, at the same locality in 1939. Now we have excellent flowering material in *Cuatrecasas 16585* which not only permits me to complete the specific description but also requires me to transfer the species to *Blakea*.

**Blakea alternifolia** Gleason, comb. nov. *Topobea alternifolia* Gleason, Bull. Torrey Club 52: 459. 1925. Petals obovate-oblong, 5 mm. long, rounded at the summit. Anthers very stout, 2 mm. long, flat and broad at the apex, opening by a dorso-terminal pore; connective much thickened toward the truncate base, not prolonged below the thecae. Sepals not triangular, as originally described, but oblate-rotund above a constricted base.

**Blakea stellaris** Gleason, sp. nov. Liana lignosa magna, ramis juvenilibus sordide furfuraceis subteretibus. Petioli 3–10 mm. longi furfuracei. Laminae late ovato-ellipticae, usque ad 10 cm. longae 7 cm. latae, superne rotundatae ad apicem breviter cuspidatum, basi cordatae, 5-nerviae, jugo marginali obscuro neglecto, supra glabrae opacae, subtus arcissime cinereo-tomentosae; venae secundariae 2–4 mm. distantes, sub angulo ca. 75° adscendentes. Flores solitarii vel bini, sessiles. Bracteae distinctae, coriaceae, ovato-lanceolatae, 7 mm. longae, 3.5–4 mm. latae, subacutae, dense tomentosae. Hypanthium campanulatum, 5 mm. longum, glabrum. Calycis tomentosi

tubus 2 mm. longus, intus ad torum dense longeque villosus; sepala triangulara, 5.4 mm. longa, acuta, extus dense intus parce tomentosa, matura stellatim patentia. Petala purpurea coriacea oblonga, 10 mm. longa 4 mm. lata, obtusa. Antherae oblongae 4 mm. longae, poris 2 dorso-terminalibus dehiscentibus; connectivum in carinam elevatum, supra basin calcare dorsali conico 0.5 mm. longo ornatum. Ovarium semi-inferum summo dense pilosum.

TYPE: *Cuatrecasas 16129*, from Peña de Candelario, on the coast of El Valle, alt. 10 m. The plant is apparently related to the Peruvian *B. sessiliflora* Naud., which also has sessile flowers with well developed sepals. In this Peruvian species the petiole is much longer, the leaf-base is acute, the leaf-surface is glabrate, the bracts are smooth, and the sepals are much shorter. *Cuatrecasas 16620* and *17189* are very similar, but deviate from the type in larger, distinctly oblong leaves broadly rounded or somewhat retuse to the apiculum and denser and shaggier tomentum. They are nevertheless referred to the same species. Sessile flowers are certainly unusual in the genus.

**Blakea pilosa** Gleason, sp. nov. Liana lignosa; rami superiores densissime pilosi, pilis adpressis usque 8 mm. longis, ad nodos densissime setosi, setis erectis usque 15 mm. longis. Petioli ca. 1 cm. longi, validi, subtus pilosi sicut caules, supra glabri. Laminae anguste oblongo-lanceolatae, 25–30 cm. longae, 8 cm. latae, acuminatae, integrae, basi cuneatae, 3-nerviae jugo marginali neglecto, supra glabrae opacae, subtus ad venas primarias densissime adpresso-pilosae, ad venas secundarias tomentosae, ad paginam glabrae; venae secundariae ca. 2 mm. distantes, sub angulo ca. 80° adscendentes. Flores 6-meri, 2 vel 3 fasciculati in quaque axilla; pedunculi 5–8 mm. longi setis longis subtenti. Bracteae omnes distinctae pilis longis subtentae, exteriores coriaceae rotundae, 9–10 mm. longae 7–8 mm. latae, interiores subrotundae 12 mm. longae 15 mm. latae. Hypanthium hemisphaericum carnosum glabrum, 5 mm. longum, pilis usque ad 8 mm. longis subtentum. Calycis tubus non evolutus; sepala ad torum distincta, late reniformia, basi imbricata, ca. 3.5 mm. longa, 7 mm. lata, dense ciliata. Petala rosea oblongo-lanceolata glabra, 17–19 mm. longa 7 mm. lata, subacuta. Filamenta 4.5 mm. longa 1.8 mm. lata. Antherae cohaerentes oblongae, 4.8 mm. longae, poris 2 terminalibus dehiscentibus; connectivum in carinam dorsalem incrassatum, basi non productum subcordatum. Ovarium summo truncato-conicum glabrum; stylus rectus 10.5 mm. longus; stigma truncatum.

TYPE: *Cuatrecasas 16532*, collected at La Trojita, in the Choco region, alt. 5–50 m. This plant represents another completely new type of structure in the genus. Its stems covered by a mass of fibers, its strongly setose nodes, even including those floral nodes bearing the bracts and flowers, its reniform, ciliate, imbricate sepals, and its narrow petals are all equally distinctive. There is no other known species with which it may be compared.

**Blakea florifera** (Gleason, sp. nov. Frutex robustus 2 m. altus, “caule quadrangulari” (mihi ignoto). Petiolus validus 19 cm. longus, dense setosus, pilis usque ad 8 mm. longis basi 1 mm. crassis. Lamina herbacea, late ovata, 44 cm. longa 33 cm. lata, abrupte acuminata, basi late rotundata, supra glabra, subtus ad paginam glabra ad venas primarias basi hispida, 9-nervia; venae secundariae ca. 5 mm. distantes. Flores 6-meri, ca. 50 in quaque axilla; pedunculi furfuracei usque ad 4 cm. longi. Bracteae distinctae membranaceae veinosae, obovato-oblongae, 11 mm. longae, apice late rotundatae,

glabrae vel fere glabrae. Hypanthium cum calyce late poculiforme, ca. 10 mm. latum, glabrum, fere truncatum; sepala ad dentes 6 triangulares 0.3 mm. longos reducta. Petala rosea, obovato-rotunda, certe 8 mm. longa.

TYPE: *Cuatrecasas 15116*, from Piedra de Moler, Cordillera Occidental, Dept. del Valle, alt. 900–1180 m. The stamens could not be dissected clearly, but seem to indicate the genus *Blakea* with little doubt. The specimen consists of a single leaf, as described above, and a longitudinal section of a part of an internode, showing a single fascicle of flowers. The great number of long-peduncled flowers is distinctive, as well as the huge broad leaves and setose petioles.

**Topobea pubescens** Gleason, sp. nov. Arbuseula epiphytica, ramis supremis subquadrangularibus, ad nodos incrassatis, dense ferrugineo-pubescentibus. Petioli validi, 2–4 cm. longi, dense pubescentes. Laminae membranaceae, late ovatae, usque ad 23 cm. longae 18 cm. latae, abrupte acuminatae in apiculum triangulare 1 cm. longum, leviter sinuato-denticulatae, basi late rotundatae cordulatae, 5-nerviae jugis binis submarginalibus neglectis, supra glabrae puncticulatae, subtus ad venas densiuscule pubescentes, ad paginam molliter stellatae; venae secundariae horizontaliter patentes 2–4 mm. distantes. Flores 2–4 in fasciculis in axillis foliorum vivorum et delapsorum; pedunculi usque ad 5 mm. longi, dense pubescentes. Bracteae exteriores 1 mm. connatae, late rotundo-ovatae vel paullo obovatae, 9–10 mm. longae 7–8 mm. latae, apiculo minuto triangulari, subtomentosae; interiores connatae 1.5 mm., rotundae, ca. 8 mm. longae lataeque. Hypanthium obconicum, ca. 6 mm. longum, parce pubescens. Calycis tubus 2.8 mm. longus, sicut hypanthium pubescens; sepala breviter triangularia, 1.1 mm. longa. Petala roseo-purpurea, inaequaliter obovata, 16 mm. longa 10 mm. lata. Filamenta tenues, 10 mm. longa; antherae lineares, 10 mm. longae, poro unico dehiscentes; connectivum vix elevatum in carinam dorsalem, basi in calcar lineare 2.8 mm. longum productum. Ovarium semi-inferum, superne productum in coronam 4 mm. longam apice in lobos filiformes 1 mm. longos fissam.

TYPE: *Cuatrecasas 16784*, collected between La Esperanza and Bellavista, Dept. del Valle, alt. 5–10 m. It is apparently related to *T. superba* Triana with similarly large leaves and bracts but nearly glabrous. A similar corona on the ovary is characteristic of *T. stephanochaeta* Naud., which is a glabrous plant with much smaller flowers and proportionately smaller bracts.

**TOPOBEA FLORIBUNDA** Gleason. I refer here *Cuatrecasas 16388*, collected in the same general region as the type. It differs from the type in its outer bracts rotund instead of acuminate, and in its leaves stellate-pubescent on the surface beneath, instead of glabrous and shining. The two come from the same general region in the Choco.

**Topobea longisepala** Gleason, sp. nov. Frutex epiphyticus, ramis ultimis teretibus arcte ferrugineo-tomentosis. Petioli 12–15 mm. longi tomentosi. Laminae chartaceae ellipticae usque ad 25 cm. longae 10 cm. latae, apice subiter in apiculum 12–15 mm. longum contractae, basi rotundatae, 5-nerviae vel sub-5-pli-nerviae jugo marginali excepto, subtus primum dense stellatae ad paginam, mox glabrescentes, ad costas tomentosae, supra primum stellatae mox glabrae; venae secundariae 2–4 mm. distantes. Pedunculi 1–3 in quaque axilla, 1 mm. longi; bracteolae 2 mm. longae, bracteis conformes. Bracteae distinctae coriaceae tomentosae rotundae vel late obovatae ca. 3 mm. longae

lataeque. Hypanthium campanulatum 2.5 mm. longum tomentosum. Calycis tubus 0.8 mm. longus; sepala adscendentia oblonga 3.5 mm. longa tomentosa. Petala ochraceo-viridia obovato-oblonga 5.5 mm. longa acuta. Filamenta gracilia 2.5 mm. longa; antherae subulatae 3 mm. longae; connectivum vix elevatum basi calcare minuto ornatum. Ovarium summo 1.3 mm. productum; stylus 3 mm. longus ad stigma punctiforme angustatus.

TYPE: *Cuatrecasas* 16975, collected at Barco, on the Pacific coast of El Valle, alt. 5–80 m. The small, almost sessile flowers densely covered with brown tomentum and with elongate sepals differentiate it from every species known to me.

**Topobea barbata** Gleason, sp. nov. Liana lignosa epiphytica. Petioli validi glabri 25–35 mm. longi. Laminae cariaceae obovatae, usque ad 15 cm. longae 10 cm. latae, superne late rotundatae vel retusae ad apiculum triangularem 2–4 mm. longum, basi late cuneatae, 5-nerviae, fere 5-pli-nerviae, jugo marginali neglecto, jugo exteriore submarginali, supra glabrae nitentes, subtus glabrae opacae, copiose nigro-punctatae, in axillis venarum 3 mediarum dense longeque barbellatae, pilis ca. 2 mm. longis; venae secundariae supra obscurae subtus vix prominulae, 1–1.5 mm. distantes, sub angulo 80° orientes. Pedunculi 1–3 in quaque axilla, usque ad 15 mm. longi, glabri, superne incrassati. Bractee brunneae glabrae coriaceae, exteriores 5.5 mm. longae 3.3 mm. connatae; interiores liberae, late oblatae, 7 mm. longae, una alteram basi fere obtegens. Hypanthium campanulatum coriaceum glabrum 6.5 mm. longum. Calycis coriacei tubus 3.7 mm. longus; sepala depresso-triangularia 1.1 mm. longa minute apiculata. Petala rosea rhomboidea 16 mm. longa. Filamenta 7.5 mm. longa; antherae crasse subulatae 6.4 mm. longae, thecis truncatis bilobulatis poris 2 terminalibus dehiscentibus, basi infra insertionem filamentum productis; connectivum non incrassatum basi in calcar conicum retrorsum 1.2 mm. longum productum. Ovarium semi-inferum, summo conicum; stylus 12 mm. longus; stigma punctiforme.

TYPE: *Cuatrecasas* 17215, collected at Barco, on the Pacific coast of Dept. El Valle, alt. 5–80 m. No described species of the genus has tufts of hairs in the vein-axils or similarly retuse leaves.

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## FICUS ALTISSIMA

MARY F. BARRETT

The objects of this paper are to differentiate between *Ficus bengalensis* L. and *F. altissima* Blume, two occasionally confused species which may show the banyan habit; to summarize the characters of *F. altissima*, and to examine its alleged synonyms and variety.

*FICUS BENGALENSIS*<sup>1</sup> L. Sp. Pl. 1059. 1753. *F. bengalensis* is believed to have been the giant species of *Ficus* seen in the Punjab, India, in 326 B.C. by the army of Alexander the Great. It has been known also as *F. indica* L. Some of its characters are almost the same as those of *F. altissima*. Differences are: crown diameter of largest trees 90-180 m., number of potential secondary trunks to 4350; petioles always hairy; blades broad-ovate or ovate-rotund; base rounded or subcordate; apex usually gradually narrowed and obtuse, rarely rounded and very short-acuminate; surfaces dull and velvety, the upper rarely becoming bare, tan or greenish-tan when dry, not papillate; 2-4 sets of apparently basal veins, 5-7 sets of secondary veins whose upper angle at midrib is about 40°; a conspicuous gland near the base of the blade; flowers said by King to have a perianth of four separate pieces; figs globose, becoming depressed at the apex, to 2 cm. in diameter, red, velvety with short white hairs; basal bracts 3, white-velvety, each about 7-8 mm. long, separate but overlapping, making a base about 12 mm. in diameter; native distribution uncertain because of extensive cultivation of the species; probably from the Indian states just south of the Himalayas, east to the head of the Bay of Bengal, south to Central India, along the west coast to Goa and Malabar.

*FICUS ALTISSIMA* Blume, Bijdr. 444. 1825. ? *Varinga latifolia* Rumph. Herb. Amb. 3: 127. pl. 84(2). 1743. *F. laccifera* Roxb. Hort. Beng. 66. 1814. *Nomen nudum*. Fl. Ind. 3: 545. 1832. *F. peguensis* Buch.-Ham. ex Wall. Cat. no. 4560 C *in part.* 1831. *Nomen nudum*. *F. varenga* Buch.-Ham. ex Wall. Cat. no. 4560 I *in part.* 1831. *Nomen nudum*. *Urostigma lacciferum* (Roxb.) Miq. Hook. London Jour. Bot. 6: 575. 1847. *U. altissimum* (Blume) Miq. ex Zoll. Syst. Verz. 2: 90. 1854. *F. altissima* var. *laccifera* (Roxb.) Trim. Syst. Cat. Ceylon 84. 1885. *F. altissima* forma *laccifera* (Roxb.) King ex Koord. & Val. Booms. Java 11: 87. 1906.

Independent or an epiphytic strangler; shrub, or tree 10-25 m., rarely to 40 m. high, crown diameter to 40 m. or more, a few secondary trunks and aerial rootlets; trunk diameter 1-5 m., to 10 m., sinuous and becoming hollow if made by strangling roots, basal buttresses and prop roots present; trunk

<sup>1</sup> This name was spelled *benghalensis* by Linnaeus, as it was an earlier polynomial by another author. The *h* seems to have been retained in texts until about 1860, but since then has usually been omitted. That there was no reason for its presence is shown by early references to Bengal, and by the title of Roxburgh's *Hortus bengalensis*, published in 1814. Linnaeus' spelling is therefore treated as an orthographic error.



bark and branches usually gray, smooth; twigs stout, gray-green to tan, white-hairy to bare; terminal buds usually 2-3.5 cm., rarely to 5 cm. long, conical, white-hairy to bare, deciduous; petioles usually 3-5 cm. long; blades usually ovate, sometimes elliptical, largest 14-17 × 8-12 cm., rarely to 30 × 21 cm.; base rounded, rarely narrowed; apex rounded and abruptly acuminate,

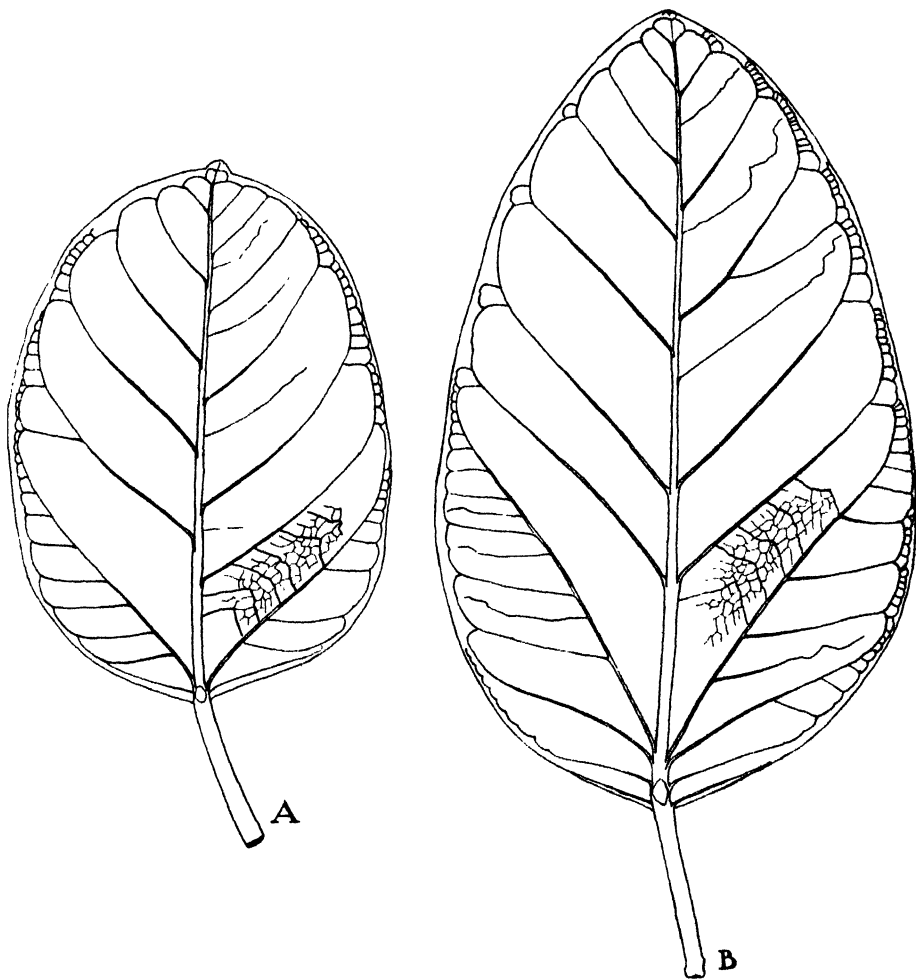


FIG. 1. Under surface of leaves of *Ficus altissima* (A) and *Ficus bengalensis* (B), showing differences in shape, apex and basal veins. Relative size is not significant.  $\times \frac{1}{2}$ . Drawings by J. Kenneth Sanders.

rarely narrowed and obtuse, the acumen short and thick; upper surface of the blade glossy, dark green with lighter colored veins, papillate; lower surface paler; blades tobacco-brown, leathery, thick and stiff when dry; a pair of basal veins making a conspicuous V of about 80°, usually a smaller pair below; 6-8 sets of secondary veins, their upper angle about 50°, forking and

uniting to form an intramarginal vein; sometimes a discontinuous tertiary vein; reticulum and checkered background present; basal gland scarcely visible; male flowers said by King to have a pedicel and 4 perianth-parts, the stamen subsessile; perianth of gall and female flowers gamophyllous, deeply 4-cleft, the styles lateral and elongate, the gall flowers pedicelled or sessile, the female flowers usually sessile; figs on leafy twigs, axillary, sessile, ovoid,  $2-3 \times 1.5-2$  cm., green becoming yellow or orange, rarely red, often sparsely papillate, velvety to bare; basal bracts 3, white-hairy, united, at first forming a calyptriform cup around the fig, later breaking off and leaving a thick pad 7-10 mm. across.

TYPE: Java.

*Distribution:* Malay Archipelago and States, Andamans, Burma, states south of the Himalayas to Northwest India, south to Central and perhaps to South India, Philippines, Indo-China, South China. Widely planted.

#### ALLEGED SYNONYMS OF *FIGUS ALTISSIMA*

*VARINGA LATIFOLIA* Rumph. Herb. Amb. 3: 127. pl. 81(2). 1743. Miquel (Fl. Ind. Bat. 1<sup>2</sup>: 349. 1859) thought that this tree was near his *Urostigma altissimum*. Koorders & Valetton (Booms. Java 11: 108. 1906) saw a resemblance between the figs in Rumphius' plate and those of *F. altissima*, and Merrill (Philippine Bur. Sci. Publ. No. 9: 194. 1917) has stated that the description represents that species or one very closely allied to it. The location of the type, Amboina, probably is within the range of distribution of *F. altissima*.

*Varinga latifolia* has been allocated to five different species, partly because of the variety of synonyms cited by Rumphius, and partly on account of its insufficient description and probably inaccurate plate. The native names are not helpful: *Waringin*, the original of *Varinga*, is applied also to other species of *Ficus*, and another local name is merely a translation of *latifolia*.

According to the description and the plate the habit is that of a large epiphytic strangler. The leaf is ovate with narrowed base and apex. There is a very short acumen. There are about 7 sets of secondary veins, all at the same angle. The figs measure about  $2.5 \times 1.3$  cm. (actual size), turn from yellow to red to black as they ripen, and are borne in a raceme.

Although such leaves are not typical, similar ones of *F. altissima* have been seen by the writer in the herbaria of the New York Botanical Garden and the Arnold Arboretum. The figs of this species may become black as they decay, although dried ones are reddish-brown. The racemous fruit cluster can not be reconciled with that of *F. altissima*, and, in fact, is rarely found among species of *Ficus*. Nevertheless *Varinga latifolia* is probably the same as Blume's species.

*FIGUS LACCIFERA* Roxb. Roxburgh gave this name to specimens collected in 1811 by M. R. Smith at "Silhet" (Sylhet in Assam), India. From that

time until 1885 the species was reported from the northeastern Himalayas as far south as southern India and Ceylon, and also from Burma and the Andaman Islands; while *F. altissima* apparently was mentioned only from the Netherlands East Indies. In 1885 Trimen declared that *Urostigma lacciferum* listed by Thwaites (Enum. Pl. Zeyl. 265. 1864) from Ceylon was, in part, var. *laccifera* of *F. altissima*. But Trimen (Handb. Fl. Ceylon 4: 87. 1898) cited *U. lacciferum* as a synonym and not a variety, adding that it was doubtful whether it was wild in Ceylon. The text of King (1887) calls *laccifera* a form, although his plates use the labels "*F. laccifera*" and "var. *laccifera*." Gagnepain (in Lecomte, Fl. Gén. Indo-Chine 5: 781. 1928) retains the name as a variety.

Roxburgh's description of *F. laccifera* differs from *F. altissima* only in glabrous stipules and glabrous figs the size of a gooseberry. The characters of the figs were ignored or changed by some later observers, but the bare stipules were frequently reported. This constitutes a slight, but in the opinion of the writer an insufficient justification for the separation of *laccifera* into a variety or form. King's statement that it is a northern form with larger, thinner leaves than those of *F. altissima* is nullified by distribution reports by Beddome (Fl. Sylv. S. India 2: 223. 1874), Brandis (For. Fl. India 418. 1874), and others; and by specimens of large leaves from trees with hairy stipules, such as have been found by the writer in Florida.

*F. PEQUENSIS* and *F. VARENGA* Buch.-Ham., both ex Wall. Ct. 1831. *Nomina nuda* were not placed by Wallich under no. 4559, *F. laccifera* Roxb.; but under no. 4560, *F. indica* Roxb. (*F. bengalensis* L.). Haines (Bot. Bihar & Orissa pt. 6. app. 1: 1248. 1924) believed that the *F. varenga* in the East India Company collection at Kew was *F. bengalensis*. But King (1887) had examined no. 4560 in four collections of the plants represented by Wallich's list, had found that specimens in the Linnean Society, Kew, and De Candolle collections did not entirely agree, but was certain that specimens of *F. peguensis* and *F. varenga* which were labeled in Buchanan-Hamilton's handwriting were true *F. laccifera*. King referred especially to the Calcutta collection.

*FICUS ALTISSIMA* Blume var. *FERGUSONII* King, Ann. Bot. Gard. Calcutta 1: 31. pl. 31 C. 1887.

Tree 24–30 m. high, air roots few, parts glabrous except for pubescent shoots; stipules lanceolate, coriaceous, 2.5–4.5 cm.; petioles 2–4 cm. long, stout; blades ovate, ovate-oblong, lanceolate or slightly obovate, 10–17.5 cm. long; base cuneate; apex cuspidate; no differentiated basal veins, 9–12 sets of secondary veins; figs axillary, sessile, subglobose, 1.3–2 cm. in diameter, orange-red, smooth; basal bracts 3, rounded, hoary, connate, at first enclosing the fig.

TYPE: *Thwaites*, Ceylon.

DISTRIBUTION: Ceylon.

King's brief description and his plate have been amplified (as above) by Trimen (1898). Willis (Rev. Cat. Pl. Ceylon 83. 1911) also speaks of the variety as native to Ceylon. No specimens have been seen by the writer.

#### SUMMARY

The main differences between two tall "banyans" with somewhat similar leaves and figs are as follows. *F. bengalensis* L. has a much more widely spreading crown than has *F. altissima* Blume, and infinitely more secondary trunks. Its leaves usually are obtuse at the apex and velvety to the touch. They commonly have two sets of large basal veins. The ripe figs are globose, red, velvety, smaller than those of *F. altissima*, and have three separate leafy basal bracts. *F. altissima* has glossy leaves with a conspicuous light-colored V made by its single set of large basal veins, and a rounded apex bearing an abrupt acumen. The figs are ovoid, usually yellow and bare, and rest on a thick pad of united basal bracts. Both species now have a wide distribution; but *F. bengalensis* probably is native only to India and neighboring states, while *F. altissima* has been found wild from India to South China.

*Varinga latifolia* Rumph., *F. laccifera* Roxb., *F. peguensis* Buch.-Ham. ex Wall., and *F. varenga* Buch.-Ham. ex Wall. are among the synonyms.

*F. altissima* var. *fergusonii* King is native to Ceylon. It differs from the type principally in its narrower blades with more and always similar secondary veins, and in its subglobose figs.

The writer is grateful to those in charge of herbaria, libraries and botanical gardens who have made this study possible.

MONTCLAIR, NEW JERSEY

## THE FERNS OF KASHMIR

RALPH R. STEWART

The native state of Kashmir is the most northerly part of the British Indian Empire. It extends roughly from 32' to 36' north latitude and from 74' to 78' east longitude. It is bounded on the west by the Northwest Frontier Province, on the north by the U. R. S. S. and Sinkiang, on the northeast by Tibet, on the east by the Punjab Himalaya, and on the south by the Punjab. Except for the famous Vale of Kashmir the whole country is mountainous. The backbone of the Himalayas forms the watershed which separates the streams flowing toward the Punjab by the Jhelum and Chenab river systems from the streams which flow into the Indus. The Indus follows a remarkable course, flowing northwest from Tibet, curving around the Nanga Parbat range in the north of Kashmir, and then cutting across the whole of the Himalayan chain to enter the plains at Attock.

That part of Kashmir which is behind the main Himalayan range and is drained by the Indus is almost rainless in summer because the high mountains check the moisture-laden monsoon winds. However, there is a heavy snowfall in winter, which produces numerous glaciers and permanent snowfields. This part of Kashmir is Tibetan in character. It is treeless, except for willows, poplars, apricots, and a few other species which are cultivated by the villagers. Except for the alpine meadows near the snowfields and the irrigated land about the villages the whole country is desert. In this region the only common fern is *Cystopteris fragilis*.

South of the Himalayas conditions are very different. There is a semi-tropical foothill zone of low xerophytic shrubs, which gradually changes as one ascends into a scrub forest in which the chief trees are *Olea cuspidata* and *Acacia modesta*. At about 3000 feet *Pinus longifolia* comes in on the ridges and steep slopes. The temperate Himalayan zone begins between 5000 and 6000 feet, where *Pinus longifolia* is replaced by *P. excelsa* and temperate hardwoods of many familiar northern genera.

The Himalayan flora extends to the limit of tree growth at from 11,000 to 12,000 feet. The position of the tree line varies with local conditions and in some inner valleys the alpine zone descends to below 10,000 feet. Above the last trees, which are commonly birches (*Betula utilis*), one usually finds shrubby junipers, willows, and rhododendrons, which are gradually replaced by the herbs of meadows, moraines, and talus slopes. The permanent snow line is at about 14,000 feet on the south slope of the Himalayas and as high as 19,000 feet on the Tibetan side.

Ferns have been collected in this region for more than a hundred years, but I have not been able to find a list of Kashmir ferns; one could be compiled from the publications of Beddome (1), Clarke (6), and Hope (9), the three men who have done most work on the ferns of North India. This list is based on their work and on the rich collections at the Dehra Dun Herbarium of the Imperial Forestry Research Institute in the United Provinces, North India, on the collections at the Royal Botanic Gardens at Kew, on the Underwood Herbarium at the New York Botanical Garden, and on the collections at Gordon College, Rawalpindi, North Punjab.

Gordon College is fortunate in possessing the Trotter collection of ferns which lay for more than forty years in a private house in Murree. It consists of about 2000 sheets of Himalayan ferns accumulated by E. W. Trotter of the Punjab Post and Telegraph Department, chiefly between 1885 and 1892. He himself collected a great many, from the Indus on the west almost to the boundary of Nepal. He obtained a large number also by exchange, thus building up an excellent working collection which includes most of the ferns known to grow between the Indus and the Burma line. He had exchanged specimens with the numerous fern enthusiasts of that golden period of fern collecting in north India, so that his herbarium contains many specimens of Gustav Mann, C. W. Hope, the Mackinnon brothers, J. C. McDonell, H. F. Blanford, Col. R. W. MacLeod, J. S. Gamble, and other contemporaries. Trotter was the discoverer of *Dryopteris (Polypodium) laterepens*.

Besides the Trotter Collection the Gordon College Herbarium contains my own collections from 1912 to 1940, those made by Prof. Mohindar Nath, and a few hundred sheets which have come in by exchange.

I have not attempted to list all the synonyms which have been used for Kashmir ferns, but only to give the correct name according to the *International Rules of Botanical Nomenclature* (ed. 3. 1935), and enough synonymy to make it possible for one using the older works of Beddome or Clarke to locate the species. I have followed the *Index Filicum* of Carl Christensen for the generic and for most of the specific names. I have not attempted to list all the specimens seen, but to cite enough from the Gordon College collections and those of the New York Botanical Garden to indicate their distribution and abundance.

A new fern flora for British India is badly needed. Beddome's *Handbook* (1), though excellent in its day, is out of date. Since 1892 much collecting has been done, many additional species have been described, and generic concepts have changed. Beddome knew the ferns of South India much better than he did those of the north. C. B. Clarke and C. W. Hope have been the outstanding students of North Indian ferns, but their publications are not readily accessible, and need revision. No one should work on the ferns of North India without C. W. Hope's *Ferns of Northwestern India* (9). He

knew the ferns in the field and saw almost all the specimens which had been collected in the area before his time. It is unfortunate that his work was not published in book form instead of in parts in the *Journal of the Bombay Natural History Society*. He checked the determinations of all the Indian specimens in the Trotter collection and those at Dehra Dun and studied the Indian collections at Calcutta, Kew, and Dublin. Little work has been done on the ferns of North India since his time. He was able to build on the work of Clarke and he described 211 ferns growing to the west of Nepal, against 149 in Clarke's Review.

Although Kashmir is not so rich in ferns as the parts of the Himalaya farther east, it has more true ferns than are to be found in the northern part of the United States and Canada as treated by Britton and Brown in their *Illustrated Flora* (4). There are 106 species and varieties in the present list. (C. B. Clarke admits 363 species for the whole of North India (omitting Lycopodiaceae and Equisetaceae), while Beddome treats 405 species and varieties. Although it is not likely that many Kashmir species have been overlooked entirely, there is still much work to be done. Many species are poorly represented in herbaria and ten per cent of the total have only been reported once. There are *Dryopteris hexagonoptera*, *D. hirtipes*, *D. marginata*, *D. macrocarpa* (*Schimperiana*), *D. repens*, *D. prolifera*, *Polystichum aristatum*, *Athyrium setiferum*, *Notholaena vellea*, *Polypodium Stracheyi*, and *Woodwardia radicans*. The first species was reported from Zaskar by Sir George Watt, and this is the only Indian record of it, but all the others grow east of Kashmir, where most of them are common. I suspect that some of them do not grow in Kashmir, but since they have been reported by Clarke or Beddome I have entered them in this list. Nine species are reported by Beddome or Clarke which neither Hope or I have been able to find in the field or in collections, and I do not know the basis of their inclusion as natives of the state. If they are really Kashmir plants I should expect to find them on the eastern border, for I have specimens of them all from farther east. They are *Dryopteris africana*, *D. repens*, *Leucostegia pulchra*, *Notholaena marantae*, *Polypodium microrhizoma*, *P. lachnopus*, *P. argutum*, *Cyclophorus porosus*, and *Diplazium maximum*. The parts of Kashmir most likely to yield new records are the southern slopes of the Pir Panjal Range from the Jhelum River to the Chamba line, especially the area nearest Chamba.

Although the fern flora of Kashmir cannot compare in richness with the area to the east where the ground ferns are supplemented by many epiphytes, yet it is quite rich in comparison with that of the British Isles, which have only 37 species, and has twice as many as are found in the Middle East. In the small area about Simla, in the Punjab Himalaya, there are 124 ferns; these were published in Collett's *Flora simlensis* (7) with identifications by Hope.

There seem to be no endemic species in the state.

A number of critical groups need further study. This is particularly true of the ferns formerly attached to *Dryopteris Filix-mas* as varieties but which are now recognized by C. Christensen and others as species, and the ferns called *Dryopteris Linnaeana* or *D. Robertiana*. More work needs to be done on the linear-leaved species commonly referred to as *Polypodium lineare* or *P. loriforme*. The ferns related to *Athyrium Filix-femina* are also difficult.

From the standpoint of distribution the most interesting fern is *Microlepia Wilfordii*, which has not been found anywhere else in India but which grows in Japan, Korea, and China. It was discovered in 1897 by McDonell in the Buniar Nullah near Rampur in the Jhelum Valley at about 4000 feet, and I found it in 1927, possibly in the same spot.

There are enough widespread northern ferns growing in Kashmir to make an American or European botanist feel at home while collecting there, especially in the temperate and alpine zone. The following, listed in Britton and Brown's *Illustrated Flora*, are also Kashmir plants, and most of them are common there.

<i>Osmunda Claytoniana</i>	<i>Asplenium trichomanes</i>
<i>Woodsia alpina</i>	<i>A. viride</i>
<i>Cystopteris fragilis</i>	<i>A. Ruta-muraria</i>
<i>C. montana</i>	<i>A. fontanum</i>
<i>Dryopteris thelypteris</i>	<i>Athyrium Filix-femina</i>
<i>D. phegopteris</i>	<i>A. acrostichoides</i>
<i>D. Linnaeana</i>	<i>Adiantum Capillus-veneris</i>
<i>D. Filix-mas</i>	<i>A. pedatum</i>
	<i>Pteridium aquilinum</i>
	<i>Cryptogramma Stelleri</i>

A number of others, not found in America, are North European ferns, while others belong to the Mediterranean flora. Four of the five ferns listed by Pampanini in his *Flora of Tripolitania* (10) are Kashmir plants. They are *Adiantum Capillus-veneris*, *Ceterach officinarum*, *Cheilanthes pteridioides*, and *Notholaena vellea*, while the fifth, *Anogramma* (*Gymnogramma*) *leptophylla*, grows to the east of Kashmir and may have been overlooked.

Of the 24 ferns in Post's *Flora of Syria, Palestine and Sinai* (11) all but five are found in Kashmir or to the east of Kashmir. Those in common are

<i>Osmunda regalis</i>	<i>Asplenium fontanum</i>
<i>Anogramma leptophylla</i>	<i>A. trichomanes</i>
<i>Ceterach officinarum</i>	<i>A. Ruta-muraria</i>
<i>Notholaena marantae</i>	<i>A. Adiantum-nigrum</i>
<i>Cheilanthes pteridioides</i>	<i>A. septentrionale</i>
<i>Pteris cretica</i>	<i>Athyrium Filix-femina</i>
<i>P. vittata</i> ("P. longifolia" Auct.)	<i>Polystichum aculeatum</i>
<i>Pteridium aquilinum</i>	<i>Dryopteris thelypteris</i>
<i>Adiantum Capillus-veneris</i>	<i>Dryopteris Filix-mas</i> vel. aff.
	<i>Cystopteris fragilis</i>



Boissier (3) describes 54 ferns found in Persia and adjacent countries, all but 18 of which grow in Kashmir.

Kashmir is just west of the area which has enough moisture during the monsoon to permit an epiphytic flora. Only a few miles to the east the zone of epiphytes begins, and the nearer one gets to the Bay of Bengal the richer the forests are in epiphytic ferns, orchids, aroids, mosses, liverworts, and lichens. From the region extending two hundred miles to the west of Kashmir only a few ferns are known which do not grow in the state, while more than a hundred others appear within two hundred miles eastward. *Adiantum aethiopicum* is the only fern I know from the Afghan frontier which does not grow in Kashmir or to the east of Kashmir. General Gatacre found 27 ferns in the Chitral region (8), of which all are Indian and 19 are European. The two most remarkable finds are *Dryopteris ludens* and *Lygodium microphyllum*, which do not grow in Kashmir but are known from farther east.

There are a number of tropical or subtropical ferns in the Kashmir foothills, but this element is not very large because of the long dry season and the small number of perennial waterfalls or streams. The Mediterranean ferns find themselves more at home here. Examples of the tropical element are *Dryopteris rampanis*, *Dryopteris dentata* (*parasitica*), *D. prolifera*, *Pteris vittata*, *Cyrtomium caryotideum*, *Polypodium membranaceum*, and *Adiantum caudatum*.

A note is perhaps necessary in explanation of the varied spelling of Indian place names. There has been an evolution in the spelling of many names. Kashmir was formerly Cashmere. Rawalpindi was Rawul Pindee. The Punjab was the Punjaub and should probably be written Panjab. The province with headquarters at Karachi has been spelled Scinde, Scind, or Sind. Even good maps differ in the spelling of names. One reason is that the natives themselves differ and another is that scientific visitors are dependent on their pony men or coolies for names and with no better guide it is not strange that variations crept in. The sound is the important thing and small differences in spelling should be overlooked.

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## POLYPODIACEAE

**WOODSIA ALPINA** (Bolton) Gray, Nat. Arr. Brit. Pl. 2: 17. 1821. *Acrostichum alpinum* Bolton, Fil. Brit. 76. 1790. *Woodsia hyperborea* R. Br. Prodr. Fl. Nov. Holl. 1: 158. 1810.

Sonamarg, 6829<sup>1</sup>; Mt. Kolahoi, 9446; Masjid Valley, Duthie 13,226; Thajwas Nullah, Duthie 13,644; Sonsal Nullah, 13,000-14,000 feet, Duthie.

An alpine plant of rock clefts. Not common.

*Distribution*: Boreal North America, central Europe, Himalaya, Altai.

**CYSTOPTERIS FRAGILIS** (L.) Bernh. Schrad. Jour. Bot. 1<sup>2</sup>: 27. 1806. *Polypodium fragile* L. Sp. Pl. 1091. 1753.

The commonest fern at high altitudes and almost the only fern in the Tibetan zone behind the Himalayas. It is usually found from 10,000 to 15,000 feet but I found it as low as 5500 feet under a rock in the Keran Nullah, Kishenganga Valley. It varies greatly in size.

*Distribution*: The Arctic and Antarctic zones and the mountains of the world.

**CYSTOPTERIS MONTANA** (Lam.) Bernh.; Desv. Mém. Soc. Linn. Paris 6: 264. 1827. *Polypodium montanum* Lam. Fl. Fr. 1: 23. 1778. *Filix montana* Underw. Nat. Ferns ed. 6, 119. 1900.

Bungas, Muzaffarabad, Inayat 20,786; Gulmarg, in woods, 9000 feet, Aitchison; Sonamarg, 10,500 feet, rock crevices in birch forest, 6868; 3-9-1884, Duthie 3647.

A rare fern at high levels.

*Distribution*: Boreal North America, Europe, Asia.

**DRYOPTERIS ROSTHORNII** (Diels) C. Chr. Ind. Fil. 289. 1905; Suppl. 3: 96. 1934. *Nephrodium Rosthornii* Diels, Engl. Jahrb. 29: 190. 1900. *Nephrodium Filix-mas* var. *fibrillosa* Clarke, Trans. Linn. Soc. II. 1: 520, *pl.* 70. 1880. *Lastrea Filix-mas* var. *parallellogramma* Bedd. Handb. 249, in part. 1883.

Sonamarg, 6340; 13,451; Khillanmarg, above Gulmarg, 10,412; Pahlgam, 8141; 8242; Keran, 17,264; Below Kel, Kishenganga Valley. Alt. 6000-11,000 feet.

This is a beautiful, shuttlecock-like form with shiny black scales. It is only once pinnate, the pinnales are very regular and only slightly denticu-

<sup>1</sup> Specimens listed without collector's name are those of the author.

late. It replaces the more eastern *D. paleacea* in Kashmir. It is very close to *D. Blanfordii* but is usually smaller, with darker ramentae and pinnules less denticulate.

*Distribution*: Himalaya, China.

**DRYOPTERIS FILIX-MAS** (L.) Schott. Gen. Fil. ad pl. 9. 1834. *Polypodium Filix-mas* L. Sp. Pl. 1090. 1753. *Nephrodium Filix-mas* Rich.; Marthe, Cat. Jard. Méd. Paris 129. 1801. *Aspidium Filix-mas* Sw. Schrad. Jour. Bot. 1800<sup>2</sup>: 38. 1801.

Hirpour, Jacquemont 586; Rembiara Valley, 6500–7000 feet, Trotter 191; Liddarwat, 9000 feet, Trotter 404; also specimens of MacLeod, Duthie, and McDonell. Cited by Hope, Jour. Bomb. Nat. Hist. Soc. 14: 727. 1903.

*Distribution*: Temperate parts of the world except Australia and southern South America.

**DRYOPTERIS BLANFORDII** (Hope) C. Chr. Ind. Fil. 254. 1905. *Nephrodium Blanfordii* Hope, Jour. Bomb. Nat. Hist. Soc. 12: 624. pl. 11. 1899. *Nephrodium remotum* of Blanford, Jour. As. Soc. Beng. 57<sup>2</sup>: 4. 1888; non Hook. 1861.

Pahlgam, 5324a; 8128; Sonamarg, 9744; 9767; 13,452; Nagmarg and Sonamarg in 1888, Trotter, cited by Hope. Alt. usually 6000–9000 feet.

Close to *D. Rothornii* when the specimens are small and the pinnules are more nearly entire than usual. The pinnae are not so regularly cut or so close together and the basal ramentae are shorter and broader and not so numerous upward on the rachis. The scales are dark, black or brownish-black. The short stipe is a good character in distinguishing this species from *D. odontoloma*.

*Distribution*: North India.

**DRYOPTERIS ODONTOLOMA** (Moore) C. Chr. Acta Hort. Goth. 1: 59. 1924; Suppl. 3: 93. 1934. *Dryopteris Filix-mas* var. *odontoloma* (Moore) C. Chr. Index 265. 1905. *Lastrea odontoloma* Moore, Ind. Fil. 90. 1858. *Nephrodium Filix-mas* var. *normalis* Clarke, Tr. Linn. Soc. II. 1: 521. pl. 71. 1880. ? *Nephrodium rigidum* Clarke, l.c. 523. *Nephrodium odontoloma* Hope, Jour. Bomb. Nat. Hist. Soc. 14: 736. pl. 31. 1903.

Batot, Jumu Road, 12,483; Between Uri and Aliabad, 13,982c; Titwal to Surkhala, Kishenganga Valley, 71,445; ? Burzil Chowki, 19,782; Sonamarg, 6334; Mitsahoi, Ladak Road, 9920a; Gilgit, 10,000 feet, in 1847, Winterbottom, cited by Hope. Alt. 3000–10,000 feet.

This is another variable fern belonging to the *D. Filix-mas* complex which is sometimes difficult to tell from *D. Blanfordii* on the one hand and *D. marginata* and *D. ramosa* on the other. It is usually twice pinnate and the stipe is long, not short as in *D. Blanfordii*. The sori are small and the pinnae are distant, increasingly so downwards. The three to five lowest pinnae are barren. The stipes are paler and more straw-colored than in *D. Blanfordii* and the fronds dry a pale color. The general outline of the frond is oblong lanceolate to ovate or deltoid lanceolate. *D. marginata* and *D. ramosa* are usually larger, tripinnate instead of bipinnate, and the general outline of the frond is more triangular.

*Distribution*: Afghanistan to Assam, Mts. of South India. China.

**DRYOPTERIS MARGINATA** (Wall.) Christ, Phil. Jour. Sci. **2**: 212. 1907. *Aspidium marginatum* Wall. List 391, nomen, in part. 1829. *Nephrodium Filix-mas* var. *marginata* Clarke, Trans. Linn. Soc. II. **1**: 521. pl. 71. 1880. *Nephrodium Filix-mas* var. *elongatum* auct. *Nephrodium marginatum* Hope, Jour. Bomb. Nat. Hist. Soc. **14**: 740. pl. 33. 1903.

Hope cites Col. MacLeod as authority for treating *D. marginata* as a Kashmir plant. MacLeod states that it is common from 6000 to 11,000 feet between the Jhelum and Kishenganga Valleys. I am not sure whether authentic *D. marginata* grows in Kashmir or not; it becomes common east of Kashmir. It is a large fern, often tripinnate, with long stipes; the outline of the frond is triangular.

*Distribution*: North India, South China.

**DRYOPTERIS RAMOSA** (Hope) C. Chr. Ind. Fil. 287. 1905. *Nephrodium ramosum* Hope, Jour. Bot. **34**: 126. 1896; Jour. Bomb. Nat. Hist. Soc. **14**: 739. pl. 32. 1903.

Dras Valley, Duthie 11,667; Pahlgam, 5725; near Gulmarg, 10,401a; 10,447; Banihal Pass, 14,089b; Sharda, Kishenganga Valley, 17,776; above Chorwan, 18,602; Badwan, 19,562; 19,602; etc.

This is the largest of the species related to *D. Filix-mas* which is common in Kashmir and largely if not completely replaces *D. marginata* in the state. Hope well states the characteristic features of the species "frond broad, hardly ever reduced at the base, pinnae, very long, broad and distant; pinnales, very long and narrow; frond pale green in color and scales almost invariably pale." It is perhaps nearest to *D. Blanfordii*, which may be distinguished by the dark ramentae, short stipe, and less compound cutting.

*Distribution*: Afghanistan to Tehri Garhwal.

**Dryopteris macrocarpa** R. R. Stewart, nom. nov. *Lastrea Filix-mas* var. *elongata* Bedd. Handb. 250. 1883. *Lastrea Filix-mas* var. *Schimperiana* Bedd. Handb. Suppl. 58. 1892. *Dryopteris cochleata* var. *Schimperiana* C. Chr. Ind. Fil. Suppl. **3**: 86. 1934. *Nephrodium Schimperianum* Hope, Jour. Bomb. Nat. Hist. Soc. **14**: 733. 1903. *Nephrodium Filix-mas* var. *Schimperiana* Clarke, Trans. Linn. Soc. II. **1**: 520. pl. 69, f. 2. 1880.

Only reported by Trotter from Rattanpir at 8000 feet. Becomes very common farther east and is one of the commonest ferns in the *Quercus incana* zone at Mussoorie. I consider it to be distinct and cannot understand why C. Christensen united it with *D. cochleata*. *D. cochleata* is dimorphic with many sterile fronds and the lower surfaces of the fertile fronds are completely hidden by the sori. This is not the case in *D. macrocarpa*. According to Christ the Ethiopian material is different from Indian "*D. Schimperiana*." See Hope, Jour. Bombay Nat. Hist. Soc. **14**: 734. 1903.

*Distribution*: Kashmir to Assam.

**DRYOPTERIS SERRATO-DENTATA** (Bedd.) Hayata, Ic. Pl. Formosa **4**: 179. pl. 116. 1914. *Lastrea Filix-mas* var. *odontoloma* of Bedd. Ferns Brit. Ind. **248**. pl. 373. 1863-5. *Lastrea Filix-mas* var. *serrato-dentata* Bedd. Handb. Suppl. 55. 1892. *Nephrodium serrato-dentatum* Hope, Jour. Bomb. Nat. Hist. Soc. **12**: 622. pl. 10. 1899. ? *Nephrodium Kingii* Hope, Jour. Bomb. Nat. Hist. Soc. **12**: 621. pl. 9. 1899.

Chatponsal Nullah, *Duthie 13,221*; Sind Valley near Baltal, *Duthie 11,613*. Both cited by Hope.

A very rare high level fern, closely related to *D. barbiger*a and *D. Brunoniana*, but more delicate. The stipes are very long for the size of the plant, being as long as or longer than the frond. The basal scales wear off more easily than they do in *D. barbiger*a.

*Distribution*: Hazara to Bhotan, China.

*DRYOPTERIS BARBIGERA* (Moore) Kuntze, Rev. Gen. **2**: 812. 1891. *Nephrodium barbigerum* Moore ex. Hook. Sp. Fil. **4**: 113. 1862. *Lastrea barbiger*a Bedd. Ferns Brit. Ind. *pl.* 227. 1867.

This is a very common and handsome alpine fern growing gregariously on alpine meadows. The fronds are broad for their length while in *D. Brunoniana* they are comparatively narrow. The stipe and rachis of *D. Brunoniana* are black or reddish-black, blacker than the scales, while those of *D. barbiger*a are pale brown, paler than the scales (Hope). Alt. 9000–13,000 feet.

*Distribution*: Afghanistan to Sikkim, China.

*DRYOPTERIS BARBIGERA* var. *Falconeri* (Hook.) R. R. Stewart, comb. nov. *Nephrodium Falconeri* Hook. Sp. Fil. **4**: 123. 1862. *Lastrea Falconeri* Bedd. Ferns Brit. Ind. *pl.* 41. 1865.

Hooker's species was based on a single frond of Falconer's from Kashmir. Clarke considered *D. Falconeri* to be the same as *D. barbiger*a, as did Beddome in his Handbook (p. 248. 1892). There are specimens like my 8642 and 10,645 from Khillanmarg, above Gulmarg with larger fronds, the pinules longer and narrower, and the rachises more glandular-resinous. Perhaps they are no more than a vigorous form of *D. barbiger*a and not worth a separate name.

*DRYOPTERIS BRUNONIANA* (Wall.) Kuntze, Rev. Gen. **2**: 812. 1891. *Aspidium Brunonianum* Wall. List 344. nomen. 1829. *Lastrea Brunoniana* Pr. Tent. 76. 1836. *Nephrodium Brunonianum* Hook. Sp. Fil. **4**: 113. *pl.* 251. 1862.

Trunkal, Gangabal Lakes, 4551; Sonamarg, 3542; 6664; Pahlgam, 5901; Mt. Kolahoi, 8275a; Khillanmarg, 8658a; 10,415; 10,422; Kamri Pass, 18,715; Zojibal to Mengandob, 18,253; Burzil to Deosai, 19,994; etc. Alt. 10,000–16,000 feet.

A common high level fern.

*Distribution*: Hazara to Bhotan.

*DRYOPTERIS CRENATA* (Forsk.) Kuntze, Rev. Gen. **2**: 811. 1891. *Polypodium crenatum* Forsk. Fl. Aegypt.-Arab. 185. 1775. *Lastrea crenata* Bedd. Ferns Brit. Ind. 18. 1876.

Not listed from Kashmir by either Beddome or Hope, but I found it between Muzaffarabad and Dhauni in the Kishenganga Valley and at Ramban, Jumu Road, 3000 feet, 10,732. There is also a specimen from the Tawi Valley, 5000 feet, by Trotter.

This is one of the finest ferns in the Himalayas and very easily recognized. It likes the sun and grows on cliffs in the outer hills, usually from 2000 to 6000 feet. The rhizome is usually wedged firmly in the rocks and the

base of the stipe is covered by long, chestnut-colored scales unlike those of any other fern in North India. Common on limestone.

*Distribution*: Cape Verde Islands to North India, Malacca, South China.

**DRYOPTERIS THELYPTERIS** (L.) A. Gray, Man. 630. 1848. *Acrostichum thelypteris* L. Sp. Pl. 1071. 1753. *Lastrea thelypteris* Bory, Dict. Class. 9: 233. 1826.

Kangan, Sind Valley, 6000 feet, 6925; 13,450. Near Dal Lake, Srinagar, 5200 feet, Thomson, Gammie, Levinge, etc.

This is a plant of springs and shallow water.

*Distribution*: Most parts of the northern hemisphere, New Zealand.

**DRYOPTERIS REPENS** (Hope) C. Chr. Ind. 288. 1905. *Nephrodium repens* Hope, Jour. Bomb. Nat. Hist. Soc. 12: 535. 1899. ? *Nephrodium prolixum* Baker, Syn. Fil. 268. 1867.

I include this in the list of Kashmir ferns on the authority of Clarke. Hope found no Kashmir specimens, nor have I. It is common from Chamba eastward.

*Distribution*: North India, Sierra Leone.

**DRYOPTERIS RAMPANS** (Bak.) C. Chr. Ind. Fil. 287. 1905. *Nephrodium rampans* Bak. Jour. Bot. 27: 177. 1889. *Polypodium lineatum* Colebr. Wall. List 300, nomen. 1829. *Goniopteris lineata* Bedd. Pr. Tent. 183. 1836. *Nephrodium costatum* of Bedd. Handb. 275. 1883.

Jhelum Valley Road, 35th mile, MacLeod; Tawi Valley, 4000 feet, Levinge; Poonch, 3000 feet, Sage, as *D. multilineatum*. Alt. 3000-7000 feet.

This plant has often been called *D. penangiana*, a plant of Malacca and Borneo (see. C. Chr. Index. Fil. Suppl. 3: 94. 1934). It is a large fern growing at low altitudes in the outer ranges on damp shady banks. The leaflets are narrower and smaller than in *D. moulmeinensis* with which it has been confused. At Mussoorie the fertile fronds come up in August.

*Distribution*: North India and China.

**DRYOPTERIS ERUBESCENS** (Wall.) C. Chr. Ind. Fil. 263. 1905. *Polypodium erubescens* Wall. List 330, nomen. 1829. *Phegopteris erubescens* J. Sm. Hist. Fil. 233. 1875.

Jhelum Valley Road, 3000 feet, Trotter; Jumu Road near Banihal Village, Kishenganga Valley, 3000 feet (Herb. Gordon); Basaoli, 5500 feet, Clarke. Alt. 3000-7000 feet.

A large fern growing in the wet ground below springs or by the side of streams, suggesting a *Pteris*. Grows in the same sort of places as *Woodwardia radicans*. Not common in Kashmir but becomes abundant farther east.

*Distribution*: North India, Malaya, South China.

**DRYOPTERIS HIRTIPES** var. **ATRATA** (Wall.) C. Chr. Contr. U. S. Nat. Herb. 26: 278. 1931. *Aspidium atratum* Wall. List 380, nomen. 1829. *Lastrea atrata* Pr. Tent. 77. 1836. *Nephrodium hirtipes* Hook. Sp. Fil. 4: 115. 1862. *Lastrea hirtipes* Moore, Ind. Fil. 85. 1858.

McDonell found this at Ghantamula in 1891 at 5300 feet and his are the only Kashmir specimens I have seen. Very rare.

*Distribution*: Himalaya, South China.

**DRYOPTERIS LATEREPENS** (Trotter) C. Chr. Ind. Fil. 274. 1905. *Polypodium repens* Trotter; Hope, Jour. Bomb. Nat. Hist. Soc. 12: 628. pl. 14. 1899.

Chittapani Valley and Rattanpir, 7500–8500 feet, Trotter; Dardpura, 4000–6000 feet, MacLeod.

This is a plant of swampy or wet ground and the type collections are in the Trotter Herbarium at Gordon College. The rhizome is necessary to distinguish it from *D. brunnea*, with which it has often been confused. All the specimens labelled *D. brunnea* in the Dehra Dun Herbarium are without rhizomes and cannot be identified with certainty; I suspect that they are really *D. laterepens*.

*Distribution*: North India.

**DRYOPTERIS LEVINGEI** (Clarke) C. Chr. Ind. Fil. 275. 1905. *Gymnogramme aurita* var. *Levingei* Clarke, Trans. Linn. Soc. II. 1: 568. 1880. *Gymnogramme Levingei* Baker, Ann. Bot. 5: 483. 1891.

Pahlgam, 7500 feet, 5334; 5489; Gulmarg, 10,206a; Surkhala to Keran, 5000–6000 feet, 17,554. Alt. 4500–9500 feet.

Like *D. laterepens*, this has a creeping rootstock and grows in damp soil. *Distribution*: Himalaya.

**DRYOPTERIS DENTATA** (Forsk.) C. Chr. Vid. Selsk. Skr. VIII. 6: 24. 1920. *Polypodium dentatum* Forsk. Fl. Aegypt.-Arab. 185. 1775. *Dryopteris parasitica* auct. non L.

Domel, 2000 feet, 5150; Garhi, 3000 feet, 5145; Chenari, 3500 feet, 12,170. All Jhelum Valley Road.

This is a common fern in the foothills up to about 3000 feet and is often called *Nephrodium molle*, *Dryopteris parasitica*, or *D. subpubescens*. The lower pinnae of *D. dentata* are gradually reduced to mere auricles, while in *D. parasitica* (L.) Kuntze the basal pinnae are unreduced. Is *D. subpubescens* a synonym?

*Distribution*: Tropical America, Atlantic Islands, Africa, Arabia, India, Tropical Asia?

**DRYOPTERIS AFRICANA** (Desv.) C. Chr. Ind. Fil. 251. 1905. *Polypodium africana* Desv. Prod. 239. 1827. *Gymnogramma totta* Schlecht. Adumbr. 15. pl. 6. 1825. *Leptogramma totta* J. Sm. Jour. Bot. 4: 52. 1841.

Reported from Kashmir by Beddome without data. I have seen no specimens. It grows from Chamba eastward.

*Distribution*: Azores, North Africa, India, Malaya, China, Japan.

**DRYOPTERIS PROLIFERA** (Retz.) C. Chr. Ind. Fil. 286. 1905. *Hemionitis prolifera* Retz. Obs. 6: 38. 1791. *Polypodium prolifera* Roxb. Wall. List 312, nomen. 1829. *Goniopteris prolifera* Pr. Tent. 183. 1836.

The only Kashmir record seems to be *Jacquemont 1419* from Rajaori in Poonch. It is a vigorous plant of the plains or low foothills, commonly growing in ditches. In 1928 I collected it at Maksud in Hazara (9653) and it probably grows in the foothills of Poonch and Jumu. It becomes common toward the east, like many other ferns which are not common in Kashmir.

*Distribution*: Tropical Africa, India, Malaya, China, Polynesia, Australia.

**DRYOPTERIS PHEGOPTERIS** (L.) C. Chr. Ind. Fil. 284. 1905. *Polypodium phegopteris* L. Sp. Pl. 1083. 1753. *Phegopteris vulgaris* Mett. Fil. Lips. 83. 1856.

Khillanmarg, above Gulmarg, 10,000 feet, 8698; Gulmarg, 8000 feet, 10,480; Sonamarg, 9000 feet, 9702; Rajdhingan Pass, 9000-10,000 feet, 18,003; 19,478. Alt. 9000-12,000 feet.

Grows in forest humus. Easily recognized by the deflexed basal pinnae and the pubescence.

*Distribution*: Temperate and arctic America, Europe, North Asia, Himalaya, Japan, etc.

**DRYOPTERIS LINNAEANA**, C. Chr. Ind. Fil. 275. 1905. *Polypodium dryopteris* L. Sp. Pl. 1093. 1753. *Phegopteris dryopteris* Fée, Gen. 243. 1850-52. ? *Gymnocarpium dryopteris* var. *disjunctum* (Rupr.) Ching, Contr. Biol. Lab. Sci. Soc. China Bot. 9: 41. 1933.

A number of specimens from Kashmir and the adjacent mountains have been referred to *D. Linnaeana*. Ching cites two Indian specimens as being his var. *disjunctum*, a Hooker and Thomson specimen from Kishtwar and Aitchison 382 from the Afghan frontier. Not having seen them, I cannot say whether they are the same as specimens hitherto referred to *D. Linnaeana* or to *D. Robertiana* in India.

*Distribution*: Temperate and arctic America; North Europe and Asia, Western Himalaya, China, Japan.

**DRYOPTERIS ROBERTIANA** (Hoffm.) C. Chr. Ind. Fil. 289. 1905. *Polypodium Robertianum* Hoffm. Deuts. Fl. 2: 20. 1795. *Polypodium calcareum* Sm. Fl. Brit. 1117. 1804. *Phegopteris Robertiana* A. Br.; Aschers. Fl. Brand. 2: 198. 1859. ? *Gymnocarpium remotum* Ching, Contr. Biol. Lab. Sci. Soc. China 9: 41. 1933.

Tragbal, 4562; Sonamarg, 7188; Aliabad Pass, 13,690; Ferozepur Nullah, 14,753; Keran to Reshna, Kishenganga Valley, 17,681; Sharda, 17,775; Chorwan to Kamri, 18,625; Rajdhingan Pass, 19,479; Chorwan to Minimarg, 19,709. Alt. 5000-11,000 feet.

There has been much difference of opinion about the two Indian oak ferns. Hope did not think it worth while to keep them distinct in India, although there are specimens which might be sorted out as one or other of the two species which are recognized in Europe. Clarke only reported one species for India but he was inclined to unite the two European forms as well. He concludes by saying: "If *P. Robertianum* be distinct it grows in the West Himalaya." Christensen recognizes both as Asiatic plants. Ching revives the generic name *Gymnocarpium* for the oak ferns and recognizes three species which he keys out as follows:

Fronde tripartito-bipinnatifid. *Eugymnocarpium*.

Habit "gracile," the two lateral divisions almost as large as the terminal; lamina perfectly naked and glabrous.

*G. dryopteris*.

Habit much stouter, the two lateral divisions much smaller than the terminal.

Lamina eglandular or sometimes only rachis, at the insertion, sparsely and shortly glandular.

*G. remotum*.

Rachis and underside of lamina always densely glandular.

*G. Robertianum*.

The Indian material does not seem to sort out satisfactorily into Ching's units, but is mostly intermediate between his *G. dryopteris* and *G. Roberti-*



*anum*. It is more glandular than his first two species and usually less glandular than his third. He states that his *G. Robertianum* is always on limestone debris but my recollection is that in India it grows usually in forest humus. It seems to me that what we have in India is a variable group of plants with some specimens almost glabrous and with the two lower pinnae almost as large as the rest of the frond, thus approaching *D. Linnaeana*, while the bulk of the material is nearer *D. Robertiana*, being more or less glandular and with the basal pinnae relatively smaller.

*Distribution*: North America, Europe, Afghanistan, North India, China.

**DRYOPTERIS HEXAGONOPTERA** (Michx.) C. Chr. Ind. Fil. 270. 1905. *Polypodium hexagonopterum* Michx. Fl. Bor. Am. 2: 271. 1803. *Phegopteris hexagonoptera* Fée, Gen. Fil. 243. 1850-52.

Only reported by Watt from Zanscar (Zaskar) a province of Ladak, behind the main Himalayan range and north of Simla. Not seen.

*Distribution*: North America.

**HYPOLEPIS PUNCTATA** (Thunb.) Mett. Kuhn. Fil. Afr. 120. 1868. *Polypodium punctatum* Thunb. Fl. Jap. 337. 1784. *Dryopteris punctata* C. Chr. Ind. 287. 1905. *Phegopteris punctata* Mett. Ann. Lugd. Bat. 1: 222. 1864.

Ramsu, Jumu-Kashmir Road, on steep bank, 4000 feet, Aug. 1931, 12,465. New to Kashmir.

*Distribution*: Widespread in the tropics of both hemispheres.

**POLYSTICHUM LONCHITIS** (L.) Roth, Röm. Mag. 2<sup>1</sup>: 106. 1799. *Polypodium Lonchitis* L. Sp. Pl. 1088. 1753.

Sonamarg, fir woods, 9000 feet, 3507; 6311; Apharwat, 11,000 feet, 8638; Rajdhian-gan Pass, 11,000-12,000 feet, 18,027; Kamri Pass, 11,000-12,000 feet, 18,692; Minimarg, Kishenganga Valley, 9000-10,000 feet, 19,159.

This has been considered to be rare in Kashmir but I find it fairly common from 9000 to 12,000 feet.

*Distribution*: Europe, colder parts of Asia and America. Northwest Frontier Province and Kashmir.

**POLYSTICHUM LACHENENSE** (Hook.) Bedd. Ferns Brit. Ind. pl. 32. 1865.

Sonamarg, 7270; 9843; Nafran near Har Nag, Upper Lidder Valley, 12,468; Zojibai Pass, 18,202; Kamri Pass, 18,727. Alt. 12,000-14,000 feet.

A plant of crevices at high altitudes. Like those of *P. Lonchitis* the old petioles of former years last over. Some smaller and more delicately cut specimens suggest *P. Thomsoni*. The species is smaller and less scaly than *P. Prescottianum*, which is a plant of open hillsides rather than rock crevices.

*Distribution*: Alpine Himalaya, China.

**POLYSTICHUM PRESCOTTIANUM** (Wall.) Moore Ind. Fil. 101. 1858. *Aspidium Prescottianum* Wall. List 363, nomen. 1829.

One of the commonest ferns in the cold temperate and alpine zone. It grows in the open and is gregarious so that there are usually dense masses on the hillside. *Dryopteris barbigera* and *D. Brunoniana*, *Athyrium Filix-foemina* var. *dentigera*, and *Osmunda Claytoniana* grow in similar places.

The fronds are narrow for their length and there are usually from 35 to 40 pairs of pinnae. Alt. 8000–13,000 feet.

*Distribution*: Abundant in the Himalaya from the Kurram Valley to Sikkim.

**POLYSTICHUM PRESCOTTIANUM** Moore var. **BAKERIANUM** W. S. Atkinson ex Clarke, Trans. Linn. Soc. II. 1: 510. *pl.* 66. 1880. *Aspidium Bakeriana* Atkinson ex Hook. Ic. *pl.* 17. 1886. *Polystichum Bakerianum* Diels in E. & P. Nat. Pfl. 1\*: 191. 1899.

Sind Valley, 12,000 feet, *Clarke*; Sarpat, *McDonell*; Trunkal, Gangabal Lakes, 11,000 feet, 18,144. Alt. 10,000–13,000 feet.

The fronds are larger and broader and the upper surface of the leaves is practically glabrous but, as Clarke felt, there is no good break between this and the typical *P. Prescottianum*.

*Distribution*: Alpine Himalaya.

**POLYSTICHUM THOMSONI** (Hook.) Bedd. Ferns Brit. Ind. *pl.* 126. 1866. *Aspidium Thomsoni* Hook. 2 Cent. *pl.* 25, in part. 1860; Sp. Fil. 4: 7. 1862.

Pushana, Winterbottom, 6500 feet; Chittapani Vy., 7500–8000 feet, *Trotter* 221; Kishtwar, *Atkinson*; Tarkiti, Indus Vy., Baltistan, 7000–8000 feet and Shyok Vy., *T. Thomson*; Har Nag, Upper Lidder Vy., rock crevices, 12,500 feet, 9342; Ascent Mir Panzil Pass to the Deosai, 12,000 feet, 20,005. Alt. 7000–13,000 feet.

This is a rather rare fern resembling a small and delicate *P. Prescottianum*. Clarke points out that the type sheet is in part *P. Prescottianum*. *Distribution*: Baltistan to Sikkim.

**POLYSTICHUM TSUS-SIMENSE** (Hook.) J. Sm. Hist. Fil. 219. 1875. *Aspidium tsus-simense* Hook. Sp. Fil. 4: 16, *pl.* 220. 1862. *Aspidium luctuosum* Hope, Jour. Bombay Nat. Hist. Soc. 14: 474. 1902. ? *Aspidium luctuosum* G. Kunze, Linnaea 10: 548. 1835–6.

Jhelum Vy., 3500 feet; Chittapani Vy., 7500–8000 feet, *Trotter*; Jhelum Vy. near Rampur, 4500 feet, *MacLeod*; Upper Chenab Vy., 6500 feet, *McDonell*; Rampur, Jhelum Vy., 12,148; Below Titwal, Kishenganga Vy., 3000 feet, 17,387. Alt. 3000–8000 feet.

*Distribution*: Temperate Himalaya, China, Japan.

**POLYSTICHUM SQUARROSUM** (Don) Fée, Gen. Fil. 278. 1850–52. *Aspidium squarrosus* Don, Prodr. Fl. Nepal 4. 1825. *Polystichum aculeatum* var. *rufobarbatum* (Wall.) Bedd. Handb. 207. 1883. *Aspidium rufobarbatum* Wall. List 369, nomen. 1828.

According to Clarke, p. 509, this fern is found from Kashmir to Bhotan and in the Nilghiri Hills. I have not found what I would call typical *squarrosus* in Kashmir, and Hope gives its distribution from Chamba eastward. *Distribution*: Himalaya, Chamba to Assam, 5000–8000 feet. Kashmir?

**POLYSTICHUM ACULEATUM** (L.) Schott, Gen. Fil. ad *pl.* 9, sensu lat. 1834. *Polypodium aculeatum* L. Sp. Pl. 1090, in part. 1753. *Aspidium angulare* Willd. Sp. Pl. 5: 257. 1810. *Polystichum angulare* Pr. Tent. 83. 1836.

Chittapani Vy., 8000 feet, *Trotter*; Dardpura, 5000–7000 feet and Aud'rbug, 7000 feet, *MacLeod*; Pir Punjal and Gulmarg, 7000 feet, *Gammie*; Rampur, 12,259a; Surkhala to Keran, Kishenganga Vy., 4500 feet, 17,493; Keran, 5000–6000 feet, 17,637. Alt. 4500–8000 feet.

This species is not as common in Kashmir as farther east. *P. aculeatum* is a "catch-all"; Hope used the name *P. angulare* for the Indian plants. Christensen says that this is a composite species which needs division but that the synonymy is very complicated.

*Distribution*: The composite species is found throughout the world in the temperate and tropical zones.

**POLYSTICHUM ARISTATUM** (Forst.) Pr. Tent. 83. 1836. *Polypodium aristatum* Forst. Prodr. 82. 1786. *Aspidium aristatum* Sw. Schrad. Jour. 1800<sup>2</sup>: 37. 1801. *Nephrodium aristatum* Pr. Rel. Haenk. 1: 37. 1825.

Trotter published a private list in which he stated that *Nephrodium aristatum* var. *affinis* Wall. List 370 had been collected in two places in Kashmir. No other Kashmir record but it is found from Chamba to Nepal.

**CYRTOMIUM CARYOTIDEUM** (Wall.) Pr. Tent. 86. pl. 2, f. 26. 1836. *Aspidium caryotideum* Wall. List 376, nomen. 1829. *Polystichum falcatum* Diels in E. & P. Nat. Pfl. 1<sup>4</sup>: 194. 1899. *Polystichum falcatum* ssp. *caryotideum* C. Chr. Ind. 202. 1905; 581. 1906.

Jhelum Valley, 3500 feet, Trotter; Chakoti, Jhelum Valley and Titwal, Kishenganga Valley, MacLeod. Alt. 3000-7000 feet.

Rare in Kashmir.

*Distribution*: Hazara east to China and Japan, Africa.

**LEUCOSTEGIA PULCHRA** (Don) J. Sm. Lond. Jour. Bot. 1: 426. 1842. *Davallia pulchra* Don, Prod. Fl. Nepal. 11. 1825.

Beddome in his Supplement, p. 13, lists *L. pulchra* for Kashmir, but I have seen no specimen. It is common from Chamba east.

*Distribution*: Himalaya, Ceylon, Yunnan.

**MICROLEPIS WILFORDII** Moore, Ind. Fil. 299. 1861.

First discovered in India by McDonell in the Buniar Nullah, near Rampur, Jhelum Valley in 1897. I found a colony on Sept. 6, 1927, below an irrigation channel, perhaps on the same spot where it was first discovered, beside the Kashmir Road at about 4500 feet (9187). The colony was still there when I last looked for it.

*Distribution*: Kashmir, Japan, China, Korea.

**ATHYRIUM CRENATUM** (Sommerf.) Rupr. Nyland. Spicil. Pl. Fenn. 2: 14. 1844. *Aspidium crenatum* Sommerf. Vet. Ak. Handl. 1834: 104. 1835.

Keran Nullah, Kishenganga Valley, in 1891, 8000 feet, McDonell; Below Gurais, 8000 feet, Duthie 12,630.

This is one of the rarest plants in the Himalaya and more material is badly needed. Hope spent a good deal of time on the question of whether it is distinct or whether it should be united with *Diplazium squamigerum*. He left the two specimens cited above in *D. squamigerum*, but his final opinion is as follows: "I have again gone over the material, and while I still think that all the Himalayan material must be identified as *A. squamigerum*, I now consider it possible that in spreading westward to Norway the Japanese plant has lost in length of sori, and become *A. crenatum*."

*Distribution*: Europe, northern and temperate Asia.

**ATHYRIUM ACROSTICHOIDES** (Sw.) Diels in E. & P. Nat. Pfl. 1<sup>4</sup>: 223. 1899. *Asplenium acrostichoides* Sw. Schrad. Jour. 1800<sup>2</sup>: 54. 1801. *Asplenium thelypteroides* Michx. Fl. Bor. Am. 2: 265. 1803. *Athyrium thelypteroides* Desv. Prodr. 266. 1827.

A very common fern, from 7000 to 10,000 feet, in damp soil.

*Distribution*: Himalaya, China, Russia, North America.

**ATHYRIUM McDONELLI** Bedd. Handb. Suppl. 34. 1892. *Asplenium McDonelli* Bedd. Jour. Bot. 27: 73. 1889.

Baniar-Harpat Rai Nala, 5000 feet, and Kitardaji, 6000 feet, *McDonell*; Lolah Valley, 4500–6000 feet, *MacLeod*; Kishenganga Vy., 6000 feet, 17,623.

This species is near *A. acrostichoides*, but the lobing of the pinnae is not so regular, there is a wider sinus between the segments, which are cut down closer to the rachis, and the rhizome is distinctly though slowly creeping.

*Distribution*: Himalaya, China.

**ATHYRIUM SETIFERUM** C. Chr. Ind. Fil. 146. 1905. *Asplenium tenellum* Hope, Jour. Bombay Nat. Hist. Soc. 12: 529. pl. 4. 1899; non Roxb. 1816 nec Fée, 1850–52. *Athyrium nigripes* of Bedd. Handb. 166. 1883.

Kishtwar, 14–11–1848, *T. Thomson*, cited by Hope. Alt. 4000–5000 feet.

*Distribution*: Northwest Himalaya.

**ATHYRIUM MACKINNONI** (Hope) C. Chr. Ind. Fil. 143. 1905. *Asplenium Mackinnoni* Hope, Jour. Bot. 34: 124. 1896.

West Kashmir, 6000–10,000 feet, in 1888, *Trotter*; *MacLeod* in 1891; *McDonell* in 1892–3; *Duthie* in 1898. All cited by Hope. Near Keran, Kishenganga Vy., 5000–6000 feet, 17,608; Below Kel, 6000 feet, 17,794; Pahlgam, 8033. The type is probably *Thomson*, Baramulla Pass, 28.8.1849. Alt. 6000–10,000 feet.

According to Hope this species includes almost all of the Himalayan specimens hitherto referred to *A. nigripes*. He does not know where to place a residue of five sheets, but states that they are not *A. nigripes*. This is a handsome fern with a pale stipe and rachis. The pinnae are attenuate at the tips and not so deeply or finely cut as in *A. pectinatum*. The stipe is long and there is an almost total absence of setae on the secondary rachises and costae.

*Distribution*: Trans-Indus to Sikkim.

**ATHYRIUM RUPICOLA** (Hope) C. Chr. Ind. Fil. 145. 1905. *Asplenium rupicola* Hope, Jour. Bombay Nat. Hist. Soc. 12: 531. pl. 5. 1899.

South slope of Pir Panjal Range, 9000 feet, *Levinge* (cited by Hope); near Bagicha, Indus Valley, Baltistan, near water-fall, Aug. 1940, 8600 feet, 20,980. Alt. 7000–12,000 feet.

*Distribution*: Kashmir to Kumaon.

**ATHYRIUM FILIX-FEMINA** (L.) Roth, Röm. Mag. 2<sup>1</sup>: 106. 1799. *Polypodium Filix-femina* L. Sp. Pl. 1090. 1753.

Sarpat, 9500 feet, in 1891, *McDonell*; near Gurais and near Gulmarg, 8000–9000 feet, in 1892, *Duthie*. Cited by Hope.

*Distribution*: North and South America, Europe, North Africa, Asia.

**ATHYRIUM FILIX-FEMINA** var. **DENTIGERA** (Wall.) Bedd. Handb. 169. 1883. *Asplenium Filix-femina* var. *dentigera* Clarke, Trans. Linn. Soc. 11. 1: 491. 1880. *Asplenium Filix-femina* var. *attenuata* Clarke l.c. 492. *Polypodium dentigerum* Wall. List 334, nomen. 1829.

This is one of the commonest ferns in Kashmir from 6000 to 11,000 feet. Clarke, p. 492, described a var. *attenuata* which he figured in *pl. 59, f. 1*. He collected the type north of the main valley, 10,000–12,000 feet. He admits that it comes near some forms of var. *dentigera* and Hope joined the two together as f. *dentigera* under *A. Filix-femina*.

*Distribution*: Kashmir to Nepal.

**ATHYRIUM FILIX-FEMINA** var. **RETUSA** (Clarke) Bedd. Handb. 170. 1883. *Asplenium Filix-femina* var. *retusa* Clarke, Trans. Linn. Soc. 11. 1: 492. 1880. *Cystopteris retusa* Dene. Jacq. Voy. Bot. 4: 176. *pl. 177*. 1844.

Sekiwas, Upper Lidder Vy., 12,000 feet, 12,475; Burzil Chowki to Mir Panzil Pass, ca. 12,000 feet, 19,945a.

*Distribution*: Himalaya, 10,000–15,000 feet, Kashmir to Bhotan.

**ATHYRIUM SCHIMPERI** Mougl. in Fée, Gen. Fil. 187. 1850–52. *Asplenium Schimperii* A. Br. in Schweinf. Beitr. 1: 224. 1867. ? *Asplenium Filix-femina* var. *polyspora* Clarke, Trans. Linn. Soc. II. 1: 493. 1880.

Basaoli, 6000 feet, Clarke 31,595; Rattanpir, 8000 feet, Trotter (cited by Hope).

This has a widely creeping rootstock and is easily distinguished. It is rare in Kashmir but becomes common farther east, especially about Mussoorie.

*Distribution*: Himalayas, Rajputana, Ethiopia.

**ATHYRIUM FIMBRIATUM** (Wall.) Moore, Ind. Fil. 185. 1860. *Aspidium fimbriatum* Wall. List 339, nomen. 1829. *Asplenium fimbriatum* Hook. Sp. Fil. 3: 234. 1860.

Sarpat, 10,000 feet, MacLeod and McDonell; north slopes of watershed between the Jhelum and Kishenganga Valleys, never lower than 10,000 feet, MacLeod (cited by Hope); above Gulmarg, 9500 feet, 10,484; Sonamarg, 10,500 feet; Pahlgam.

This is the largest of the Kashmir Athyriums and has a creeping caudex. Clarke writes that it is common from 5000 to 12,000 feet but in Kashmir it does not seem to have much altitudinal range, growing near 10,000 feet.

*Distribution*: Kashmir to Bhotan, Yunnan.

**DIPLAZIUM POLYPODIOIDES** Bl. Enum. 194. 1828. *Asplenium polypodioides* Mett. Fil. Lips. 78. 1856.

Clarke, Trotter, McDonell, cited by Hope without data. Near Kangan, Sind Valley, by spring, 6000 feet, 6924.

One of the largest ferns in Kashmir but not so common as farther to the east. In some places the young shoots are cooked.

*Distribution*: North India, Malaya, Tropical Australia.

**DIPLAZIUM JAPONICUM** (Thunb.) Bedd. Ferns Br. Ind. Suppl. 12. 1876. *Asplenium japonicum* Thunb. Fl. Jap. 334. 1784. *Athyrium japonicum* Copeland, Bish. Mus. Bull. 93: 43. 1932.

Keran, 5500 feet, Kishenganga Valley, *McDonell 33, 34*; Mardan Ali in 1854 (Herb. Dehra) (cited by Hope).

*McDonell 34* in New York is without rhizome and suggests *Athyrium McDonelli*. The rhizome is creeping, the stipe may be longer than the rest of the leaf.

*Distribution*: Tropical Asia, including India, China, Japan, etc. Australia.

**DIPLAZIUM SQUAMIGERUM** (Mett.) Christ, Bull. Soc. Fr. **52**, Mém. 1: 51. 1905. *Asplenium squamigerum* Mett. Ann. Lugd. Bat. **2**: 239. 1866.

Sharda, Kishenganga Vy. by stream, 6000 feet, *17,751*; Below Kel, Kishenganga Valley, 6300 feet, *17,818*. Hope cites several collections of McDonell and Duthie, all apparently from the extreme west of Kashmir between 7000 and 9000 feet.

This is a very rare fern in India and suggests *Athyrium crenatum* var. *glabratum* Ching. It has a black creeping rhizome, the frond is almost tri-pinnate, triangular, and with the stipe is about two feet high. The scales are dark, broad, ovate-lanceolate, and the pinnules crenate. Hope considers this intermediate between typical *A. crenatum* and *Diplazium squamigerum*. *Distribution*: Japan, China, North India.

**ASPLENIUM VIRIDE** Huds. Fl. Angl. 385. 1762.

Shish Nag, Lidder Vy., 13,000 feet, *Trotter*; Kamri Vy., 10,000–11,000 feet, *Duthie 12,552*; Gangabal Lakes, 12,000 feet, *4479*; Sonamarg, 12,000 feet, *6562*; 10,500 feet, *6869*; Baltal, 9500 feet, *7528*; Shish Nag Pass, 11,000–13,000 feet, *8407*; Near Gadsar, 11,000–12,000 feet, *18,309*; Kamri Pass, *18,712*; Minimarg, 9000–10,000 feet, *19,187*.

A fairly common rock plant at high altitudes.

*Distribution*: Europe, Himalaya, North America.

**ASPLENIUM TRICHOMANES** L. Sp. Pl. 1080. 1753.

One of the commonest ferns in Kashmir forests and found also in the inner ranges. Gilgit, Baltistan, Kamri Pass, etc., from 4000 to 12,000 feet. *21,019* was found in Baltistan between Bagicha and Olthing Thang near the Indus at 8500 feet, close to a waterfall; *17,373* in the lower Kishenganga Valley at 3000 feet, the lowest altitude at which I have found it.

*Distribution*: Widespread in north and south temperate regions and on tropical mountains.

**ASPLENIUM SEPTENTRIONALE** (L.) Hoffm. Deuts. Fl. **2**: 12. 1795. *Acrostichum septentrionale* L. Sp. Pl. 1068. 1753.

Nagmarg, 9000 feet, *Trotter*; Sonamarg, 9000 feet, *3442*, 10,000 feet, *6600*; Kishenganga Valley, 6000–8000 feet, *17,740*, *17,888*, etc.

This is another common rock crevice plant. It grows in tufts and may be mistaken for a grass by the uninitiated. Usually from 6000 to 10,000 feet, but has been found up to 14,000 feet.

*Distribution*: Europe, North Asia, Himalaya, U. S. A.

**ASPLENIUM RUTA-MURARIA** L. Sp. Pl. 1081. 1753.

Sonamarg, 11,000 feet, *7192*; 9200 feet, *9865*; Taobat, Kishenganga Valley, 7500 feet, *17,865*; Badwan, Kishenganga Vy., 8000 feet, *19,599*, etc.; Kangi, Nullah, above Kangi, Ladak, 13,500 feet, *Koelz 2528*; Shingo Vy., Baltistan, 10,000–11,000 feet, *Duthie* fide Hope.

*Distribution*: Europe, North Asia, Himalaya, U. S. A., etc.

**ASPLENIUM SEPTENTRIONALE** × **TRICHOMANES** Murbeck, Lunds. Univ. Årsskr. 27: 35. 1892. *Asplenium germanicum* of C. Chr. Ind. Fil. 113. 1905, non Weis. 1770.

Pahlgam, on large boulder, 7200 feet, 7883; Kishenganga Vy., McDonell fide Hope; Jerdon, Herb. Kew, as *A. germanicum*.

One of the rarest of Kashmir plants.

*Distribution*: Europe, Kashmir, Hongkong.

**ASPLENIUM SARELII** Hook. in Blakiston, Yang-tsze 363, 364. 1862. *Asplenium pekinense* Hance, Jour. Bot. 5: 262. 1867. *Asplenium Saulii* Baker, Syn. Fil. ed. 2. 216. 1874. *Asplenium Saulii* var. *pekinense* Bedd. Handb. Suppl. 31. 1892.

4000 feet, Trotter 371; Rampur to Uri, MacLeod; 2200 feet, Leringe; 3600 feet, McDonell. All on the Jhelum Valley Road.

A very rare fern and one of the most finely cut of the *Aspleniums*. In India it has only been found from Hazara to Kulu.

*Distribution*: Himalaya, China, Japan.

**ASPLENIUM ADIANTUM-NIGRUM** L. Sp. Pl. 1081. 1753.

Tangmarg, below Gulmarg, 7200 feet, 10,709; below Titwal, 3000 feet, 17,373; Titwal to Surkhala, 4000 feet, both in the Kishenganga Valley; below Tragbal, 7000 feet, 19,466, etc.

Usually from 4000 to 7000 feet in comparatively dry places in the outer valleys. Much more common than *A. Sarelii*.

*Distribution*: Temperate Asia, Europe, Atlantic Islands, African Mts., etc.

**ASPLENIUM FONTANUM** (L.) Bernh. Schrad. Jour. Bot. 1799<sup>1</sup>: 314. 1799. *Polypodium fontanum* L. Sp. Pl. 1089. 1753.

Sonamarg, rock crevices by the Sind River, 8000 feet, 3419; 10,000 feet, 7229; Lidderwat, 9000 feet, 8301; Aru to Nafran, Lidder Vy., 9000 feet, 12,470; Kishenganga Valley, 3000-7000 feet, 17,408; 17,456; 17,695; 17,838; 19,600; etc. Alt. 3000-12,000 feet.

Fairly common in rock crevices.

*Distribution*: Western Himalayas, Europe, Central Asia.

**ASPLENIUM VARIANS** Wall. Hook. & Grev. Ic. Fil. pl. 172. 1830. *Aspidium varians* Wall. Ms. in Herb. Hook.

Pahlgam, 8000-9000 feet, Duthie 13,466; Sonamarg, 9200 feet, 6437; Baltistan, near Skardu, Thomson, fide Hope; Near Bagicha, Baltistan, Indus Vy., 8500 feet, 21,002. Alt. 4000-9000 feet.

Not so common in Kashmir as it becomes farther east. It is not so finely cut as *A. fontanum* and grows in humus rather than in rock crevices.

*Distribution*: India to China and Japan, Africa, Hawaii.

**CETERACH DALHOUSIAE** (Hook.) C. Chr. Ind. Fil. 170. 1905. *Asplenium alternans* Wall. List 221, nomen. 1829; Hook. Sp. Fil. 3: 92. 1860.

Very common at lower levels on the outer ranges especially from 3000 to 7000 feet, growing on banks and walls. Alt. 3000-9000 feet.

*Distribution*: Himalaya, Ethiopia.

*CETERACH OFFICINARUM* DC. in Lam. & DC. Fl. Fr. 2: 566. 1805. *Asplenium Ceterach* L. Sp. Pl. 1080. 1753. *Hemidictyum Ceterach* Bedd. Ferns Brit. Ind. Suppl. 13. 1876.

Mt. behind Dal Lake, 7000 feet, 3284; Jhelum Valley Road, 4000 feet, 12,120; Dhanni, 2800 feet, 17,366; Dhanni to Titwal, 3500 feet, 17,372, both in Kishenganga Valley; Gilgit, Tanner and Astor Dist, Duthie fide Hope. Alt. 3000-8000 feet.

Like *C. Dalhousiae* this is a xerophytic fern of the outer ranges and grows in the same sort of places. The lower surfaces of the fronds are densely covered with scales which are absent in *C. Dalhousiae*.

*Distribution*: Central Europe, the Mediterranean basin, Western Asia. South Africa, Western Himalaya.

*WOODWARDIA RADICANS* (L.) Sm. Mém. Ac. Turin 5: 412. 1793. *Blechnum radicans* L. Mant. 307. 1771.

Basaoli, 5500 feet, Clarke. The only specimen reported by Hope. Alt. 3500-7500 feet.

The only place in which I have found it common in Kashmir is in the lower Kishenganga valley from Mugaffarabad to Titwal, Chenab Vy., Ramsu to Banihal. It becomes commoner as one goes east, growing in shady woods along streams. The fronds are long and arching and root from bulbils at the tips of the leaves or along the axis.

*Distribution*: Atlantic Islands, Mediterranean Basin, North India, South China, Java.

*GYMNOPTERIS VESTITA* (Wall.) Underw. Bull. Torrey Club 29: 627. 1902. *Grammitis vestita* Wall. List 12, nomen. 1829. *Gymnogramma vestita* Pr. Tent. 218, nomen. 1836. Hook. Ic. pl. 115. 1837. *Syngramma vestita* Moore, Ind. Fil. 60. 1857.

I have seen no specimens from Kashmir, but since I have specimens from Hazara on the west and from various places on the east, it has most probably been overlooked. This is one of the few ferns especially sought by European visitors in the Himalayan Hill Stations. It is called mouse ear fern.

*Distribution*: China, North India.

*CRYPTOGRAMMA STELLERI* (Gmel.) Prantl, Engl. Jahrb. 3: 414. 1882. *Pteris Stelleri* Gmel. Nov. Comm. Petr. 12: 519. pl. 12, f. 1. 1768. *Pellaea gracilis* Hook. Sp. Fil. 2: 138. pl. 133 B. 1858. *Pellaea Stelleri* Bak. Syn. Fil. ed. 1. 453. 1868.

Karakorum Mts., Baltistan, Thomson; Gurais, Kishenganga Vy., Duthie; Gangabal Lakes, 11,000 feet, 18,138; Mt. Kolohoi, Upper Lidder Vy., 12,000 feet, 13,444; Chuna-gund, Ladak, 9000-10,000 feet, 21,059; Sonamarg, Tulion, Nafran, etc.

A plant of the alpine zone, usually from 9000 to 12,000 feet. One of the few ferns to cross the Himalayas into Baltistan and Ladak.

*Distribution*: Siberia, Himalaya, North America.

*CRYPTOGRAMMA BRUNONIANA* Wall. List. 396, nomen. 1829; Hook & Grev. Ic. Fil. pl. 158. 1829. *Cryptogramma crispa* of Bedd. Handb. 98. 1883.

Sonamarg, 11,000 feet, 6572; above Gulmarg, 11,000 feet, 10,416; ascent from Burzil Pass to Deosai, 13,000 feet, 19,986; Muzaffarabad, Inayat; Marbal Pass, Clarke, etc. Alt. 10,000-15,000 feet.



Another alpine plant like the last but easily recognized by the dimorphic fronds, the fertile fronds being erect and taller.

*Distribution*: Himalaya, China, Japan.

CONIOGRAMME FRAXINEA (Don) Diels in E. & P. Nat. Pfl. 14: 262. 1899. *Diplazium fraxinea* Don, Prodr. Fl. Nepal. 12. 1825. *Gymnogramma javanica* Blume, Enum. 112. 1828. *Syngramma fraxinea* Bedd. Handb. 386. 1883.

Jhelum Valley Road, 4500 feet, Trotter; Rattanpir, 7500-8000 feet, Trotter; Hajipir Pass, 8000 feet, 13,996; Kishenganga Valley, 3000 feet, by dripping bank, 17,492.

The last specimen and Bliss 57 from the same valley approach *Coniogramme affinis* (Wall.) Hieron, the low level form farther east, as some fronds have only the lowest pinnae divided. High-level Kashmir specimens are much more compound with narrower leaflets.

*Distribution*: India, China, Japan, Australia, Polynesia, Tropical Africa, Madagascar.

PELLAEA HASTATA (Thunb.) Prantl, Engl. Jahrb. 3: 418. 1882. *Pteris hastata* Thunb. Prod. Fl. Cap. 172. 1800. *Pteris calomelanos* Sw. Link. Fil. Sp. 61. 1841.

Abbottabad, Hazara, 4500 feet, 14-7-1934, 14,112.

This fern has hitherto not been reported this far west in India. It has been reported from Simla and since it has now been found to the west of Kashmir it may be expected in the state.

*Distribution*: Himalaya, Hazara to Kumaon; Yunnan, Ethiopia to the Cape of Good Hope.

PELLAEA NITIDULA (Wall.) Baker, Syn. Fil. 149. 1867. *Pteris nitidula* Wall. List. 89, nomen. 1829. *Cheilanthes nitidula* Hook. Sp. Fil. 2: 112. 1852.

Poonch; Kishtwar, 5000 feet, Clarke; Chittapani Valley, 6000 feet, Levinge; Pir Panjal, 6000 feet, and Rattanpir, 8000 feet, Gammie. All cited by Hope. Alt. 3000-9000 feet.

A plant of the outer ranges. Superficially like *Cheilanthes subvillosa* but lacks the hairs.

*Distribution*: Afghan Frontier to Kumaon, Yunnan, West Tibet.

NOTHOLAENA MARANTAE (L.) R. Br. Prodr. Fl. N. Holl. 146. 1810; Jour. de Bot. Appl. Desv. 1: 92. 1813. *Acrostichum Marantae* L. Sp. Pl. 1071. 1753.

Reported from Kashmir by Clarke and Beddome but without definite data. I have seen no Kashmir specimens, but since it grows near by in Kulu and Chamba, it may grow on the eastern border of the state.

*Distribution*: Atlantic Islands, Mediterranean Basin, Himalaya, Yunnan.

NOTHOLAENA VELLEA Ait. Jour. de Bot. Desv. Appl. 1: 93. 1813. *Acrostichum vellea* Ait. Hort. Kew. 3: 457. 1789.

The only Kashmir specimen I have seen was a sheet of Jerdon's at Kew marked Cashmire. It is a very rare fern in India and only three specimens are in the Dehra Herbarium and two at Gordon College, all from the Punjab Himalaya in the vicinity of Pangi, Kulu, and Chamba.

*Distribution*: Atlantic Islands and Mediterranean Basin to Afghanistan and the Northwest Himalaya.

**CHEILANTHES PTERIDIODES** (Reich.) C. Chr. Ind. Fil. 178. 1905. *Polypodium pteridioides* Reich. L. Syst. Pl. ed. novis. 4: 424. 1780. *Polypodium fragrans* L. Mant. 307. 1771, non 1753. *Cheilanthes fragrans* Webb & Berth. Hist. Nat. Canar. 3<sup>2</sup> (3): 452. 1847.

Jhelum Valley, near Pirni, 5000–6000 feet, *Duthie*; Kishtwar, 3500–5000 feet, *Clarke*; both cited by Hope; Domel, Jhelum Valley Road, 2500 feet, 11,100; Kishenganga Valley, 3500–6000 feet, 17,413; 17,436; 17,550.

This is one of the most xerophytic of Kashmir ferns and grows in the drier outer ranges. At Titwal, Kishenganga Valley, it grew in the crevices of the walls of terraced fields near *Asplenium Adiantum-nigrum*, *Ceterach Dalhousiae*, and *Ceterach officinarum*.

*Distribution*: Atlantic Islands, Mediterranean Basin, Northwest Himalaya.

**CHEILANTHES PERSICA** (Bory) Mett. Kuhn, Fil. Afr. 73. 1868. *Notholaena persica* Bory, Bél. Voy. Bot. 2: 23. 1833. *Cheilanthes Szovitzii* Fisch. & Mey. Bull. Soc. Mosc. 6: 260, nomen. 1833; 241. 1838.

Skardu, Baltistan, 8000 feet, 20,428; Kiris, Indus Valley Baltistan, 8000 feet, 20,891; Takht, Srinagar, 6000 feet, 9465; Rampur, Jhelum Valley, 4000 feet, 12,128; Martand, Kashmir, 5200 feet, McDonell; Kishtwar, *Clarke*.

This is a fern from the Mediterranean flora which penetrates deep into the Himalayas as far as Gilgit and Baltistan. It is one of the few ferns able to live in the low hills of the north Punjab and Northwest Frontier Province. The species is easily separated from the last by the abundant red woolly hairs from the sori which cover the lower surfaces of the pinnules.

*Distribution*: Mediterranean Basin to the Northwest Himalaya.

**CHEILANTHES SUBVILLOSA** Hook. Sp. Fil. 2: 87. pl. 98B. 1852.

Chittapani Valley, 9000 feet, and Rattan Pir, 8000 feet, *Trotter*. Alt. 7000–10,000 feet.

Few specimens from Kashmir are in collections. It should be looked for on the southern slopes of the Pir Panjal Range. It can easily be separated from *Pellaea nitidula*, which it resembles, by the hairs on the lower surface of the veins.

*Distribution*: Northwest Himalaya from Hazara to Sikkim.

**CHEILANTHES ALBOMARGINATA** Clarke, Trans. Linn. Soc. II. 1: 456. pl. 52. 1880. *Cheilanthes farinosa* var. *albomarginata* Bedd. Handb. Suppl. 22. 1892.

Although this is a very common fern east of Kashmir the only one who seems to have found it within the state was Clarke, who found it at Basaoli at 5000 feet.

*Distribution*: Himalaya, South India.

**CHEILANTHES DALHOUSIAE** Hook. Sp. Fil. 2: 80. pl. 78B. 1852. *Cheilanthes farinosa* var. *Dalhousiae* Bedd. Handb. 93. 1883.

Clarke reports this from Kashmir but without data and Hope does not mention any Kashmir specimens. I have only found it near the Indus River in the vicinity of Bagicha, Baltistan, at about 8500 feet, 20,961 and 21,003 in Aug. 1940.

Although this plant has been referred to *C. farinosa* it is without white powder at all stages. The involucre are deeply crenulate, toothed or lacerate. *Distribution*: Himalaya, Hazara to Sikkim.

CHEILANTHES FARINOSA (Forsk.) Kaulf. Enum. 212. 1824. *Pteris farinosa* Forsk. Fl. Aegypt.-Arab. 187. 1775.

Jhelum Valley, between Domel and Chakota, *MacLeod*; Kaman Goshi, 3000 feet and Tawi Valley, 4000 feet, *Gammie*, the only specimens reported by Hope.

I found this near Domel at 2000 feet in Aug. 1931. It becomes common east of Kashmir and as it is not rare in Abbottabad, Hazara and grows in Rawalpindi Dist. it probably grows on the south slopes of the Pir Panjal Range.

*Distribution*: India, China, Japan, Africa, Tropical America, Fiji.

ONYCHIUM LUCIDUM (Don) Spr. Syst. 4: 66. 1827. *Leptostegia lucida* Don. Prodr. Fl. Nepal 14. 1825. *Onychium contiguum* Hope, Jour. Bombay Nat. Hist. Soc. 13: 444. 1901. *Onychium japonicum* var. *multisecta* F. Henderson ex Clarke, Trans. Linn. Soc. II. 1: 459. 1880. *Onychium japonicum* var. *lucidum* Christ.

Rattan Pir, 8000 feet, *Trotter*; Pir Panjal, 8000 feet, *Gammie*; cited by Hope; Aliabad Pass, Pir Panjal Range, 7000-8000 feet, 13,991. I have also found it on the Batot Pass at about 6000 feet.

*Distribution*: North India, China.

ADIANTUM CAUDATUM L. Mant. 308. 1771.

This is perhaps the commonest fern in the foothill zone of the Northwest Himalaya and begins at the edge of the plains and ascends to about 5000 feet, rarely to 6000 feet. It penetrates into Kashmir by the Jhelum Valley and the Tawi Valley of Jumu. It is no doubt common in Poonch and the outer spurs of the Pir Panjal Range but I have seen no specimens. It roots freely at the tips.

ADIANTUM CAPILLIS-VENERIS L. Sp. Pl. 1096. 1753.

One of the commonest ferns in North India and one of the two or three ferns which are found in the plains of the Punjab. It is common in wells and wet banks in the plains and in the hills it frequents waterfalls and springs. It occasionally penetrates deep into the Himalayas. I found one poor specimen in Baltistan, and *Koelz* 2821 was collected at 12,500 feet in the Kangi Nullah, Ladak.

*Distribution*: Europe, Africa, temperate Asia, Polynesia, Central America, etc.

ADIANTUM VENUSTUM Don, Prodr. Fl. Nepal 17. 1825.

This is probably the commonest forest fern between 6000 and 9000 feet and it may be found from 4000 to 12,000 feet.

*Distribution*: Afganistan, North India.

ADIANTUM PEDATUM L. Sp. Pl. 1095. 1753.

Ashdari, Padar, Kishtwar, 8000 feet, 2901; Tragbal, 9000 feet; Aru, Lidder Valley, 8500 feet; Sharda to Kel, Kishenganga Valley, 6500 feet, 17,803; Gulmarg, 8500 feet, *Martin*. Alt. 6500-10,000 feet.

Not rare; but the "stag-horn fern" is not found every day. It needs deeper shade and richer, damper humus than is required by *A. venustum*.  
*Distribution*: Japan, China, Japan, North America.

*PTERIS VITTATA* L. Sp. Pl. 1074. 1753. *Pteris longifolia* L. and many authors, in part.

One of the commonest ferns in the foothill zone and up to 5000 feet in the outer hills. Found even in the plains by running water; and the commonest potted fern in the Punjab. This fern has usually been called *P. longifolia* in India, but according to Carl Christensen this name belongs to a tropical American fern.

*Distribution*: More tropical parts of Europe, Africa, Asia, Australia, and Polynesia.

*PTERIS QUADRIAURITA* Retz. Obs. 6: 38. 1791. *Pteris biaurita* var. *quadriaurita* C. Chr. Ind. Fil. 605. 1906.

Rattanpir, 7500-8000 feet, Trotter.

This fern becomes very common farther east.

*Distribution*: India, Ceylon.

*PTERIS CRETICA* L. Mant. 130. 1767.

This is another very common fern in the drier, outer ranges at altitudes of from 3000 to 7000 feet. The difference between the fertile and sterile fronds is striking. The pinnae of the sterile fronds are wider and have spinulose margins.

*Distribution*: Atlantic Islands and Mediterranean Basin to the Philippines and New Zealand; West Indies, Brazil, etc.

*PTERIS EXCELSA* Gaud. Freyc. Voy. Bot. 388. 1827.

The only Kashmir record is a doubtful one. Hope states that a sterile specimen of Gammie's from Rattanpir referred to *P. quadriaurita* might be a sterile specimen of *P. excelsa*. Since *Inayat* 20,432 from the Siran Valley, Hazara, comes from west of Kashmir, and this is a common fern eastward, it is most probable that it will be found on the Pir Panjal Range.

*Distribution*: North India and Malaya to Fiji and Hawaii.

*PTERIDIUM AQUILINUM* (L.) Kuhn; v. Deck. Reisen 3<sup>s</sup>: Bot. 11. 1879. *Pteris aquilina* L. Sp. Pl. 1075. 1753.

Common on sunny grassy hillsides or forest openings from about 6000 to 9000 feet. In the Kishenganga Valley it begins as low as 3000 feet in grassy openings in the *Pinus longifolia* forest and continues in suitable places to above 9000 feet on the Kamri, Burzil, and Rajdhangan Passes, where it enters the *Artemisia maritima* zone. It may grow to be six feet tall.

Tryon (*Rhodora* 43: 22. 1941) refers the Indian material to var. *Wightianum* (Ag.) Tryon. He cites my 4761 and 6492 as being more glabrous than most specimens of the variety.

*Distribution*: Temperate and tropical regions of the world.

*POLYPODIUM MICRORRHIZOMA* Clarke, Baker Syn. Fil. 511. 1874. *Goniophlebium microrrhizoma* Bedd. Ferns Brit. Ind. Suppl. 21. pl. 384. 1876.

Beddome in his handbook gives the distribution "Kashmir to Bhotan." I have collected it in Dalhousie a few miles to the east but have seen no Kashmir specimens.

*Distribution*: Himalaya, Yunnan.

*POLYPODIUM LACHNOPUS* Wall. List 310, nomen. 1829; Hook. Ic. *pl.* 952. 1854. *Goniophlebium lachnopus* J. Sm. Hook. Gen. Fil. ad *pl.* 51. 1840.

Clark and Beddome both mention this as a Kashmir plant but I cannot find any specimens. I have many specimens but the nearest are from Simla and Kulu. This fern is often mixed with the last but can be recognized by the abundant, dark, long pointed ramentae clothing the creeping rhizome. Both this and the last are usually epiphytes.

*Distribution*: Himalaya.

*POLYPODIUM ARGUTUM* Wall. List 308, nomen. 1829; Hook. Sp. Fil. 5: 32 1863. *Goniophlebium argutum* Hook. Gen. Fil. ad *pl.* 51. 1840.

This is another epiphyte which according to Beddome in his Handbook, p. 324, grows from Kashmir to Bhotan. I have seen no specimens.

*Distribution*: Simla Hills to Sikkim.

*POLYPODIUM MEMBRANACEUM* Don, Prodr. Fl. Nepal 2. 1825. *Pleopeltis membranacea* Moore, Ind. Fil. 191. 1860.

Jumu, Tawi Valley, 4000-5000 feet, Trotter; Gamme, 4000 feet.

Like the three previous ferns this becomes common as soon as the monsoon is sufficient to make epiphytes possible.

*Distribution*: Eastern Kashmir to the Philippines, and Celebes, Ceylon.

*POLYPODIUM STRACHEYI* (Ching) C. Chr. Ind. Fil. Suppl. 3: 159. 1934. *Phymatodes Stracheyi* Ching, Contr. Inst. Bot. Nat. Acad. Peiping 2: 83. 1933. *Polypodium Stewartii* Clarke, Trans. Linn. Soc. II. 1: 563. 1880; non *Pleopeltis Stewartii* Bedd. 1867.

Pahlgam in rock crevices, 10,000 feet, Aug. 8, 1927, 9276.

New to Kashmir. Previously the westernmost station of this plant was the Sach Pass in Chamba.

*POLYPODIUM LORIFORME* Wall. List 271, nomen. 1829; Mett. Abf. Senckenb. Ges. Frankfurt 2: 92 *pl.* 1. *f.* 50. 1857. *Polypodium lineare* var. *steniste* Clarke, Trans. Linn. Soc. II. 1: 559. 1880. *Polypodium lineare* var. *loriforme* Takeda, Notes Bot. Gard. Edinb. 8: 272. 1915. ? *Lepisorus loriformis* Ching, Bull. Fan. Mem. Inst. 4: 81. 1933.

Liddarwat, 9000 feet, 8278; Pahlgam, 8323; Ferozepur Nullah, near Gulmarg, 7500 feet, Sonamarg, 13,464.

I have puzzled over these specimens; 8323 may be different. In it the lower side of the frond is completely covered by the large sori. This is not the case in the other specimens but it may be a matter of age. The leaves are thicker than those of *P. clathratum* and when dry the veins are still invisible. The leaves of *P. clathratum* seem thin when dried, they are greener in color, and the veins are visible, though the freshly picked fronds are fairly thick and take a long time to dry. *P. excavatum* Bory, with which it

has sometimes been confused, is thin-leaved even when fresh and dries quickly. It is usually an epiphyte and I have not found it in Kashmir. Clarke does not mention clathrate scales in *P. loriforme*, but they are present. I suspect that the Chinese and Japanese material of Ching and Takeda may be different.

*Distribution*: North India, South China?

POLYPODIUM CLATHRATUM Clarke, Trans. Linn. Soc. II. 1: 559. *pl.* 82. *f.* 1. 1880. *Pleopeltis clathrata* Bedd. Handb. 348. 1883.

Pahlgam, 5950; Lidderwat, above Pahlgam 9000 feet, 8253; Sonamarg, 9500 feet; 10,000 feet, 13,455; Aru to Nafran, Lidder Valley, 9000 feet, 12,469; Nittar Valley, Gilgit Dist, in 1892, Duthie. Alt. 9000-12,000 feet.

This is a fairly common rock plant at high levels in Kashmir in the shade of forest trees. The clathrate scales remain on the rhizome after they have fallen from the old sori. The leaves dry very slowly. They are usually much narrower and somewhat shorter in length than in *P. excavatum* which it sometimes resembles superficially. *P. excavatum* is usually an epiphyte and the leaves die at the close of the monsoon, while *P. clathratum* has evergreen leaves, like *P. loriforme*.

*Distribution*: North India, North China. Afghanistan.

CYCLOPHORUS POROSUS (Wall.) Pr. Epim. 130. 1849. *Polypodium porosus* Wall. List 266, nomen. 1829; Mett. Pol. 128. n. 259. 1857. *Nipholobolus porosus* Br. Tent. 202. 1836. *Nipholobolus fissus* of Bedd. Ferns Brit. Ind. Correct. 2. 1870.

"From Kashmir to Bhotan, very common." Clarke. In my experience this fern grows from Kulu and Chamba eastward and I have seen no Kashmir specimens. Some botanists use the name *Pyrrosia* for this genus.

*Distribution*: North India, China.

#### SCHIZAEACEAE

LYGODIUM JAPONICUM (Thunb.) Sw. Schrad. Jour. 1800<sup>2</sup>: 106. 1801. *Ophioglossum japonicum* Thunb. Fl. Jap. 328. 1784.

"Near Domel, Jhelum Valley, in great profusion," MacLeod; Poonch Valley, 3000 feet, Winterbottom; Tawi Valley, 3500 feet, Gammie. Alt. 2500-5000 feet.

Apparently very local. I have found it at Mansera in Hazara and in Chamba but the only *Lygodium* I have found in Kashmir was a sterile plant from Ramban on the Jumu to Srinagar Road.

*Distribution*: India, China, Japan; tropical Asia and Australia.

#### OSMUNDACEAE

OSMUNDA CLAYTONIANA L. Sp. Pl. 1066. 1753.

Common in large patches on open hillsides and in open places in the forest from 8000 to 11,000 feet. Has been reported at 6000 feet.

*Distribution*: Himalaya, China, North America.

#### SALVINIACEAE

SALVINIA NATANS (L.) All. Fl. Pedem. 2: 289. 1785. *Marsilia natans* L. Sp. Pl. 1099. 1753.

Very common in the lakes and canals in the Valley of Kashmir at about 5000 feet.

*Distribution*: India, Central China, Europe.

#### MARSILIACEAE

*MARSILIA MINUTA* L. Mant. 308. 1771 (excluding  $\beta$ ). *Marsilia erosa* Willd. Sp. Pl. 5: 540. 1810.

Very common in rice fields and shallow water from the plains to about 6000 feet. The leaves which form in a dry period are smaller and are often erose at the tip.

*Distribution*: India, Java, Philippines.

#### OPHIOGLOSSACEAE

*OPHIOGLOSSUM VULGATUM* L. Sp. Pl. 1062. 1753.

Cited for Kashmir by Clausen, Mem. Torrey Club 19: 127. 1938.

I have an *Ophioglossum* from Pahlgam, in grass, 7500 feet, which probably belongs here.

*Distribution*: North America; Europe to India. Japan, Kamtchatka.

*BOTRYCHIUM LUNARIA* (L.) Sw. Schrad. Jour. 1800<sup>2</sup>: 110. 1801. *Osmunda lunaria* L. Sp. Pl. 1064. 1753.

Western Tibet, Falconer and Karakorum Mts., Clarke, cited by Clarke; Mt. Apharwat, above Gulmarg, 11,000 feet, in rocks, 8587; Pahlgam, in forest, 7500 feet, 9232.

*Distribution*: Colder portions of both northern and southern hemispheres.

*BOTRYCHIUM VIRGINIANUM* (L.) Sw. Schrad. Jour. 1800<sup>2</sup>: 111. 1801. *Osmunda virginiana* L. Sp. Pl. 1064. 1753.

Lolab Valley, R. C. Wroughton, U. S. Nat. Herb. cited by Clausen; Canon Stokoe, Chaplain of Srinagar, has a specimen from Pahlgam, Lidder Valley. Hope states that Inayat 20,388 from the Kaghan Valley, Hazara is typical *B. virginianum*.

There has been a great deal of discussion about the presence or absence of *B. virginianum* in India. Clarke maintained that there was only one species and he called it *B. virginianum*. Beddome in his Handbook, p. 471, mentions only one form which he calls *B. virginianum* var. *lanuginosum*. Probably Clarke had only *B. lanuginosum*, which is the common Himalayan plant east of Kashmir. The only note I have of the presence of *B. virginianum* east of Kashmir is the statement of Trotter that McDonell found it in Chamba. Clausen places the Kashmir specimen in subsp. *typicum*.

*Distribution*: North America, Europe, India, China, Japan.

#### EQUISETACEAE

*EQUISETUM ARVENSE* L. Sp. Pl. 1516. 1753.

Very common in Kashmir. In the Kishenganga Valley I have seen the young fertile stems push up as soon as the snow melted. It is found at Ganderbal in the main valley and penetrates to Dras and Ladak. Alt. 5000–12,000 feet.

*Distribution*: North America, Europe, North and Central Asia.

*EQUISETUM DEBILE* Roxb. Vauch. Monog. Prel. 376. 1822.

Srinagar, 5200 feet, 13,458; below Sharda, Kishenganga Valley, in sand, 6000 feet. 17,730; Rupal Nullah, Astor Dist., 8000 feet, 18,884 (possibly *E. ramosissimum*).

*Distribution*: India, Ceylon, Malaya, Polynesia.

**EQUISETUM RAMOSISSIMUM** Desf. Fl. Atlant. 2: 398.

Very common, penetrating into the inner valleys of Ladak and Baltistan. It is found from the plains to 9000 feet. Not very different from *E. debile* but more scabrous, the cones usually single, not approximated, the secondary cones more nearly sessile and the basal branches from the main stem ascending rather than at right angles to it.

*Distribution*: Widespread in the northern hemisphere.

## LYCOPODIACEAE

**LYCOPODIUM SELAGO** L. Sp. Pl. 1102. 1753.

Sonamarg, 13,000 feet, among dwarf rhododendrons, 7336 (f. *angustinum* Christ, det. Nessel); above Gulmarg, 12,000–13,000 feet, 8609; Burzil, 10,000 feet, Koelz 9410; Gilgit, 12,000 feet, Duthie?

*Distribution*: North America, Europe, North Asia.

## SELAGINELLACEAE

**SELAGINELLA SANGUINOLENTA** (L.) Spring, Monog. Lycopod. 2: 57. 1849.

*Lycopodium sanguinolentum* L. Sp. Pl. 1104. 1753.

Sonamarg, 8–8–1928, 10,000 feet, 9458, det. Alston.

*Distribution*: North India.

**SELAGINELLA JACQUEMONTII** Spring, Monog. Lycopod. 2: 194. 1849.

In determining 6660, 7173, and 7368, Alston refers this species to *L. sanguinolenta* as a variety. Baker and Hieronymus, on the other hand, in their monographs made *S. Jacquemontii* a synonym of *S. borealis* Spring. The species or variety is common in the Kishenganga Valley on cliffs from 3000 to about 8000 feet, 17,381, 17,458, 17,833, 17,888a, and 17,878 all seem to belong here.

*Distribution*: North India.

**SELAGINELLA AITCHISONI** Hieron. in E. & P. Nat. Pfl. 14: 674. 1901.

Pahlgam, 5959; Sonamarg, 6791; Baltal, 7464. Alt. 7000–11,000 feet.

All det. by Alston. He refers this form to *S. sanguinolenta* as a variety and the new combination will probably be published in his monograph in due course.

*Distribution*: North India.

## REJECTED SPECIES

**DRYOPTERIS BRUNNEA** (Wall.) C. Chr. Ind. 255. 1905. *Polypodium brunnea* Wall. List 333, nomen. 1829. *Phegopteris distans* Mett. Pheg. Asp. 16 n. 23. 1858. *Polypodium distans* Don. Prodr. Fl. Nepal 2. 1925.

Specimens referred to this are probably *D. laterepens*.

**DIPLAZIUM MAXIMUM** (Don) C. Chr. Ind. Fil. 235. 1905. *Asplenium maximum* Don, Prodr. Fl. Nepal 8. 1825. *Asplenium latifolium* Don, Prodr. Fl. Nepal 8. 1825. *Athyrium maximum* Copel. Bish. Mus. Bull. 59, 54. 1929.

Clarke reports this fern from Kashmir under the name of *Asplenium latifolium*. He gives no data and I do not think that it grows in the state. Hope thought that he had *Diplazium polypodioides*, to which this is related.

*Distribution*: Tropical Asia, Polynesia, Australia.



# INDEX TO AMERICAN BOTANICAL LITERATURE

## PLANT TAXONOMY AND FLORISTICS (exclusive of fungi)

(See also under Morphology: **Castellanos; Occhioni**)

- Alexander, E. J.** *Gentiana linearis*. Native of northeastern North America. *Addisonia* 22: 43, 44. *pl.* 726. 4 Ap 1945.
- Alexander, E. J.** *Gerardia acuta*. Native of northeastern North America. *Addisonia* 22: 33, 34. *pl.* 721. 4 Ap 1945.
- Alexander, E. J.** *Habranthus Andersonii*. Bronze fairy-lily. Native of Texas, Argentina, Uruguay and Chile. *Addisonia* 22: 45, 46. *pl.* 727. 4 Ap 1945.
- Alexander, E. J.** *Rubus linkianus*, double white bramble. Native of Europe? *Addisonia* 22: 35, 36. *pl.* 722. 4 Ap 1945.
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- Castellanos, A. & Lelong, H. V.** *Opuntia Weberi* Speg. var. *dispar* Castell. et Lelong. *Lilloa* 10: 469, 470. *pl.* 29 D 1944.
- Castellanos, A. & Lelong, H. V.** Una nueva especie de *Opuntia*. *Lilloa* 10: 395-402. *pl.* 1-3. 29 D 1944.
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- Everett, T. H.** *Fritillaria pudica*. *Addisonia* 22: 37, 38. pl. 723. 4 Ap 1945.
- Everett, T. H.** *Kalanchoe grandiflora*. Native of India. *Addisonia* 22: 41, 42. pl. 725. 4 Ap 1945.
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## INHERITANCE OF ORANGE AND YELLOW FLOWER COLOR IN *NEMESIA STRUMOSA*

HERBERT PARKES RILEY

In 1929 the author undertook to study the interaction of the genes that produce the many different flower colors in *Nemesia strumosa*. This work was carried on until 1932 as a graduate student in Dr. Geo. H. Shull's laboratory at Princeton University and was continued for the next two years as a National Research Council fellow in the biological sciences at the Bussey Institution of Harvard University under the late Dr. E. M. East. By 1934, seventeen genes for flower color had been identified at least tentatively, and a report showing that self-sterility is determined by oppositional factors was published the following year (Riley 1935). The results of the study of the inheritance of flower color were not published at that time, however, because it was considered desirable to investigate several points more thoroughly and to check more carefully several possible linkage relationships. An abstract describing briefly five of the genes was published in 1940 and one showing that two flower color genes are linked with the self-sterility alleles was published in 1944.

*Nemesia strumosa* Benth. is a South African plant of the Scrophulariaceae which has been in cultivation in this country since the last part of the nineteenth century (Bailey 1937). Although Bailey states that this species is of easy cultivation, the author has found that this is true only within certain limits. Most of the plants used for this study were grown in the greenhouse during the winter. In general they grew very well, but on some occasions they appeared highly susceptible to certain fungi, and in each of two years several hundred plants were lost before flowering because of an attack of *Botrytis cinerea*. During another year, a large number of plants was lost when the greenhouse was fumigated with formaldehyde. Some plants were grown out-of-doors but this species frequently does not stand the summer heat in New Jersey or New England very well, and Taylor's (1936) statement that it is "essential for them to make as much growth as possible before summer heat" is appropriate.

After carrying on this study for several years, the author moved to a location where he had no facilities for growing plants during the winter months and where the summer climate was too hot for *Nemesias*. After several attempts to continue this problem, it was given up. Four years later, he again moved to a more suitable location and attempted to resume these studies. During three successive years, the seeds of a number of the old

pedigrees were sown in a greenhouse in the usual manner but apparently the delay had been too long, for not one seed had remained viable. The author then obtained new lots of seeds and has continued the study with these new plants; but unfortunately, several of the old flower-color types have not been secured as yet in the new material.

#### MATERIALS AND METHODS

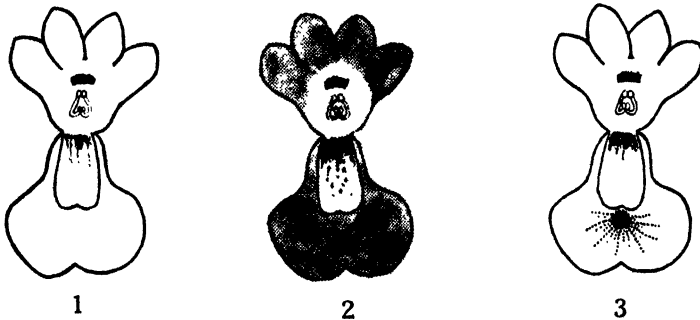
The original plants were grown from a seed packet purchased from Peter Henderson and Co. in New York in 1929 and labelled, "Nemesia—Newton's Glories mixed." Twelve plants were selected for the original crosses, and all families of the earlier part of this study were descendants of these plants. These twelve plants were apparently heterozygous for a great many genes, for 75 different phenotypes were described and catalogued from the  $F_1$  generation of 13 crosses among these original plants. Subsequently, it was found that a few of these 75 phenotypes were fluctuations and that some others were the result of modifying genes of slight effect which could not be readily analyzed, but most of these types represented genes or combinations of genes which could be at least partially analyzed. The original plants were photographed in color on lantern slides, while later generations were recorded in water color and by descriptions based on a comparison with Ridgway's (1912) color charts. With a few exceptions, all crosses were guarded and the usual precautions of the pedigree culture method were observed.

After it was learned that seed from the original lines was no longer viable, a number of new lots of seeds were purchased and sown. In 1940, packets of seeds of *N. strumosa* Suttoni including "Blue," "Orange," "Pink," "Scarlet," "White," "Yellow," and "Mixed Colors" were purchased from Peter Henderson and Co., while packets of *N. grandiflora* Suttoni mixed, of *N. compacta* (= *N. versicolor*) "Triumph," and of *N. compacta* "Blue Gem" were purchased from the Ferry-Morse Seed Co. In 1943, new lots of "Blue," "Orange," "Pink," "Scarlet," "White," and "Mixed Colors" of *N. strumosa* Suttoni were obtained from Peter Henderson and Co., while lots of *N. strumosa* "Tall Blue," and of *N. compacta* "Fire King" were purchased from Herbst Bros. in New York.

The flower of *Nemesia strumosa* has a corolla with a short tube which bears a short spur or pouch. The limb of the corolla is two-lipped and the upper or posterior lip is strongly notched so that it has four distinct parts. The lower or anterior lip usually has one shallow notch in the center. There are four didynamous stamens which usually cohere about the stigma (fig. 1). The corolla limb on the inside may be white, orange, yellow, or several shades of red and purple; there may be a blue margin on the upper lip, or it may be spotted or streaked with red. The lower part of the tube may be

orange or straw-color and may have a few or many dots of very deep purple. The upper part of the tube is generally colorless, but above the stamens there frequently is formed a large spot of very deep purple, which the author calls the "eyebrow." Apparently these colors all exist in wild plants (Bailey 1937), and apparently a very large number of interacting genes is present.

A genetic analysis of this species is rendered somewhat difficult by the fact that it is self-sterile (self-incompatible). Because of the presence of self-sterility alleles, it is impossible to obtain seed by self-fertilizing mature flowers, and it is sometimes impossible to make certain crosses because the plants to be crossed have the same self-sterility alleles. All families, therefore, arose from sib crosses or from crosses between plants of two different families. When dealing with a typical heterozygous  $F_1$  generation it makes



FIGS. 1-3. Diagrams of flowers of *Nemesia strumosa*. Each flower is cut along both sides of the tube and is then flattened out. This causes some distortion of the tube but little distortion of the lips. FIG. 1. The white-flowered, standard type. FIG. 2. Orange; the shaded areas show the distribution of the orange pigment in the lips. FIG. 3. Yellow spot; the approximate distribution of the pale yellow pigment on the lower lip is indicated by the dark spot and radiating lines.

no difference whether an  $F_2$  generation is produced from it by the self-fertilization of one plant or by a cross between two sibs. However, this is not the case when seeds from other than typical  $F_1$  generations are desired, for in such families plants that are alike phenotypically do not necessarily have the same genotype. This is an important consideration in this *Nemesia* study, for the original plants were mostly heterozygous for a large number of the genes and the families which arose from crosses among them were therefore not typical heterozygous  $F_1$  families. Since it was impossible to self-fertilize individual plants, subsequent generations had to be produced by crossing two plants, and there was no assurance that two plants were alike genotypically even though they were sibs and were alike phenotypically. For example, in several instances it was desired to determine whether the offspring of a dominant type would segregate into a 3:1 or some other ratio. If the family to be tested were from seeds of unknown ancestry, it is possible that

some of the dominants might be homozygous; if the species is self-fertile, the chance of securing a heterozygote for breeding by self-fertilization would be only two in three plants. When the species is self-sterile, segregation of the offspring will be obtained only when two heterozygotes are crossed. In a family segregating in a 3:1 ratio, the chance of obtaining two heterozygotes simultaneously is only four out of nine, which shows that the chances of a successful test, when the original parents are not homozygous, is considerably less in a self-sterile species than in a self-fertile one.

A further complication arises if some of the genes to be tested happen to be linked with the self-sterility alleles for, in self-sterile species, genes which determine morphological characters do not give typical mendelian ratios in certain crosses if they are linked with the self-sterility alleles. In 1926, Brieger and Mangelsdorf showed that the basic color gene *C* in *Nicotiana* is so linked; and Williams (1935, 1937) subsequently showed that five genes in red clover are on chromosome-II in addition to the self-sterility alleles. Anderson and De Winton (1931) found that in hybrids of *Nicotiana Langsdorffii* and *N. alata* at least one gene for corolla-tube length is linked with the self-sterility alleles. They found also that at least one of the several pairs of genes that determine differences in the proportionate length of the style in *Nicotiana* and one of the pairs of alleles that determine pollen color in crosses between *N. Langsdorffii* and *N. alata* appear to be strongly linked with the self-sterility alleles.

Linkage with self-sterility genes is important because of gametic elimination in certain crosses. If two plants are mated that have no self-sterility allele in common, as in the cross  $s^1s^2 \times s^3s^4$ ,<sup>1</sup> there will be no gametic elimination; if each of these plants is also heterozygous for a gene determining some morphological character, the offspring will segregate in a monohybrid ratio for that character whether or not the self-sterility alleles and this other gene are linked. If, on the other hand, the two plants have one self-sterility allele in common, the result will be different. If there is complete linkage, and if the dominant morphological gene of the male parent is on the same chromosome as the common self-sterility allele, the offspring will segregate into a ratio of one dominant to one recessive. Such a cross is  $s^1A/s^2a \times s^1A/s^3a$ . Because of the elimination of the  $s^1$  pollen, the two resulting types of offspring will be  $s^1A/s^3a$  and  $s^2a/s^3a$ . If linkage is not complete, the ratio will be less than 3:1 but greater than 1:1, and there will be an excess of recessives. If the recessive morphological gene in the male is coupled with the common self-sterility allele and if linkage is not complete, there will be an excess of dominants, as in the cross  $s^1A/s^2a \times s^1a/s^3A$ .

In backcrosses in which there is linkage between the genes for self-steril-

<sup>1</sup> Superscripts rather than subscripts are used in this paper to designate self-sterility alleles. See de Haan (1932) and Riley (1932).

ity and those for morphological characters, reciprocal crosses do not always give the same results. If a homozygous recessive female is crossed with a heterozygous male in which the dominant gene is coupled with the common self-sterility allele, there will be an excess of recessives in the offspring. In the cross,  $s^1a/s^2a \times a^1a/s^3A$ , there will be an excess of dominants. In each case, the reciprocal cross will yield a ratio of one dominant to one recessive.

#### OBSERVATIONS

**White.** In the white-flowered plants, the inner parts of both lips of the corolla are white, while the lower part of the tube is Orange<sup>2</sup> or Orange Chrome. Deep purple spots may be present or absent on the lower part of the tube and the "eyebrow" may or may not be present. The cells of the corolla lips are mostly papillate and there are few, if any, hairs. In the lower part of the tube, the papillae are longer than in the cells of the lips. Almost all the cells of the lower part of the tube appear to be completely filled with deep yellow pigment. When examined microscopically, the papillae of the cells seem to be of a deeper color than are the remaining parts of the cells, but this probably is merely the result of a greater thickness of the cell at that place. When white flowers are placed in ammonia vapor, the corolla lips begin to turn yellow at once. When the color change has been completed, they are Lemon Yellow, and all the epidermal cells when examined under the microscope are yellow. The orange tube does not change color. In hydrochloric acid vapor, the lips become Orange-Buff on the inside, but in dilute nitric acid they appear to remain unchanged.

The white-flowered type will hereafter be regarded as the standard type. This is not to be understood as a wild-type in the sense in which the word is applied in *Drosophila*, for many of the other types occur frequently in nature and some perhaps as frequently as does the white-flowered type. This type, however, will be used as a type of reference or a standard from which other types will be regarded as departures or mutants.

**Orange (O).** Like the white-flowered plants, the orange-flowered type is common. The "orange" color is probably very deep yellow (fig. 2) rather than orange, and may be lightened in color by at least two principal modifying genes in addition to others of small effect.<sup>3</sup>

In orange-flowered plants that are not affected by these principal modifying genes, the lips are usually either Light Cadmium or Cadmium Yellow, although in a few plants the color seems close to Orange. The orange color is

<sup>2</sup> Colors are capitalized which are standardized from Ridgway (1912).

<sup>3</sup> In a preliminary report (Riley 1940), the author called this type yellow and used the symbol *Y* to designate the dominant gene for this color. He has learned subsequently, however, that this type is sold commercially as orange rather than yellow. In order to conform to that practice, he will designate this type as orange hereafter and will substitute the symbol *O* for the *Y* of the preliminary paper.

confined to the epidermal cells. These cells are papillate and the water-soluble orange pigment appears to fill the whole cell. The tube is the same as that of the white-flowered type. When placed in ammonia vapor, there is no change in either the lips or the tube. When the orange-colored epidermis is stripped off, however, exposing the colorless subepidermal layers, the exposed portions turn Lemon Yellow. In HCl vapor, the orange color of the lips and tube becomes paler and in some cases fades out almost entirely. In sulfur dioxide the lips remain unchanged and the orange color of the tube becomes very slightly paler.

Orange behaves as a simple dominant over white. In 16 families which resulted from a cross between two orange types, 377 orange and one white plant were produced. It is not unlikely that the white was an interloper. In 12 of these 16 families, one or both parents contained anthocyanin pigment in addition to the orange pigment, but in tabulating the ratio of orange to white, only plants lacking anthocyanin were included. Twenty-eight families were the result of crosses between two non-orange plants one or both of which may also have contained an anthocyanin pigment. The offspring that did not contain anthocyanin included 759 white-flowered but no orange-flowered plants. Crosses between apparently homozygous orange and non-orange plants produced seven families which contained 443 orange and one white-flowered plants, not including those with anthocyanin. Again, this lone white plant may have been an interloper.

That orange is dominant is shown by the fact that in seven families of different parentage, orange  $\times$  non-orange gave orange. It was desirable to confirm the dominance of orange by crossing two heterozygotes but this test was not set up until 1933 and it was not possible to raise the seeds from those crosses. Seven families from crosses between orange and non-orange yielded a total of 104 orange- and 104 white-flowered plants. In no family was the deviation as great as twice the standard error. The symbol for orange will be *O*.

Linkage between the orange gene and the self-sterility alleles has not been tested, since the self-sterility alleles of one parent in five of these test-crosses was unknown, while in the other two crosses, the self-sterility groups of both parents were undetermined.

**Pale-upper (*p*).** This type appears to be a modification of orange and has several expressions depending, perhaps, upon other genes. Typically, the lower lip is Light Cadmium and the upper lip is Apricot Yellow or Empire Yellow, or between them in color. In some plants that appear to be genetically similar to the typical form, both lips are Light Cadmium, but this deep yellow color of the upper lips is largely restricted to the central part of the lobes and almost completely fades out at the edges. In some plants, the upper lips are Maize Yellow with some spots of Buff Yellow or of Light Cadmium

on the inner parts. The lower part of the tube is Orange, as in the white and orange types, and may or may not have deep purple spots. The gene for pale-upper seems to affect only gene *O*, for pale-upper and non-pale-upper cannot be differentiated in *oo* plants. In one cross, a white plant was crossed with a pale-upper which was heterozygous for *O*. The offspring segregated into 14 deep orange : 11 pale-upper (orange) : 30 white. The appearance of the deep orange type from a white  $\times$  pale-upper cross indicates that white and pale-upper do not differ by just a single pair of genes.

That pale-upper is recessive to orange is shown in a number of cases. Eight families resulting from a cross between two plants apparently heterozygous for pale-upper and of which at least one was *OO* segregated into 285 orange and 110 pale-upper against an expected ratio of 296:99. In no family was the deviation more than twice the standard error. Nine families

TABLE 1. *Observed ratios of orange (non-pale-upper) to pale-upper in eight families in which one self-sterility allele was common to the two parents, and the corresponding expected ratios based on the absence of linkage between the pale upper gene and the self-sterility alleles.*

Family	Parents	Genotypes of parents	Observed		Expected		Dev. S.E.
			<i>P</i>	<i>p</i>	<i>P</i>	<i>p</i>	
3103	3001 (6) $\times$ (22)	<i>ssvupp</i> $\times$ <i>svszPp</i>	13	8	10.5	10.5	1.09
3105	3001 (8) $\times$ (22)	<i>ssvupp</i> $\times$ <i>ssszPp</i>	10	0	5.0	5.0	3.10
3225	3103 (1) $\times$ (5)	<i>svszpp</i> $\times$ <i>ssszPp</i>	7	9	8.0	8.0	0.50
3223	3103 (3) $\times$ (52)	<i>svszPp</i> $\times$ <i>ssszPp</i>	16	9	18.8	6.2	1.30
3226	3103 (5) $\times$ (3)	<i>ssszPp</i> $\times$ <i>svszPp</i>	20	2	16.5	5.5	1.72
3361	3103 (52) $\times$ (4)	<i>ssszPp</i> $\times$ <i>ssszPp</i>	7	0	5.2	1.8	1.55
3362	3103 (52) $\times$ (40)	<i>ssszPp</i> $\times$ <i>svszPp</i>	26	10	27.0	9.0	0.38
3411	3103 (4) $\times$ (52)	<i>svszPp</i> $\times$ <i>ssszPp</i>	5	3	6.0	2.0	0.82

resulted from crosses between a heterozygote and a pale-upper plant. While the total consisted of 114 orange and 78 pale-upper, in only one of the families did the ratio of the deviation to the standard error exceed 2, and in this family the number of individuals was small. It seems reasonably certain that pale-upper is recessive to orange; the symbol *p* will be used to designate this gene.

Evidence on linkage between the pale-upper gene and the self-sterility alleles is not so abundant as might be desired, but the data that are available indicate that there is no linkage. In three test-crosses in which the parents had a common self-sterility allele and the male parent was heterozygous for *P*, only one family showed a ratio of which the deviation was more than twice as great as the standard error (table 1). In five families in which both the parents were heterozygous for *P* and had one self-sterility allele in common, the deviation was less than twice the standard error. These eight families do not indicate any linkage relationship between pale-upper and self-sterility.

Little evidence is available to indicate whether *o* and *p* are linked, but what evidence there is is negative. Two families resulted from the cross  $OoPp \times ooPp$ . Since *P* and *p* cannot be differentiated in the *oo* plants, the test for linkage is whether the orange and pale-upper types segregate into a 3:1 ratio. In these families the ratios were 7:2 and 21:5. Since neither differs significantly from a 3:1 ratio, there is some evidence that *o* and *p* are not linked.

**Buff (*bu*).** Like pale-upper, buff appears to be a modification of orange and is rather variable in expression. Most typically, the lower lip of the corolla is Light Cadmium near the throat, but most of the lip is Buff Yellow and the edges may be as light as Sulphur Yellow; the upper lip is Sulphur Yellow with areas of Buff Yellow. In some plants of the buff type, the paler regions of the lips are Baryta Yellow, and the deeper places are Empire Yellow. The lower part of the tube is Orange and may or may not have deep purple spots. Buff gives the general appearance of being much paler than pale-upper.

Buff is a modification of orange, and is not expressed in *oo* plants. In plants with the *O* gene, buff appears to be recessive to non-buff. In a number of crosses between two non-buff plants, only non-buff offspring appeared, while in one cross between two buffs there were 27 buff and no non-buffs. Four families arose from a cross between two heterozygotes and produced a total of 122 orange (non-buff) : 54 buff, and in no family was the deviation twice as great as the standard error (table 2). In three backcrosses of a non-buff to a buff, the ratio was 18 non-buff : 23 buff, and in no family did the ratio of the deviation to the standard error exceed 2. That buff and white are not the result of allelic genes is shown from two families in which a white that apparently was homozygous for non-buff was crossed with a buff heterozygous for *O*. In one family, the ratio was 26 orange (non-buff) : 17 white, while in the other family it was 9 orange (non-buff) : 12 white. If white and buff differed merely by a single gene, orange-flowered (non-buff) plants would not have been recovered from a white  $\times$  buff cross. Buff, then, is apparently recessive to non-buff and is independent of gene *O*. The gene for buff will be designated by the symbol *bu*.

Four other families arose from crosses between two *Bu bu* plants but each exhibited a very poor fit to a 3:1 ratio (table 3). If, however, the buff gene is linked with the self-sterility alleles with about 5 per cent crossing over, the observed ratios are much closer to the expected. If family 3103 arose from the cross  $s^*bu/s^*Bu \times s^*Bu/s^*bu$ , the  $s^*$  male gametes would be eliminated. Except for crossing over, these would also be *Bu* gametes, so the expected ratio would be close to 1:1 with a slight excess of non-buff plants due to crossing over. The observed ratio was 21 non-buff : 23 buff which is much closer to the expected ratio based on linkage than to that based on no linkage.



Families 3104, 3105, and 3106 arose from similar crosses in which the *Bu* gametes were eliminated in the male except for those that arose by crossing over. While these families are rather small, they deviate much less from the expected ratios based on linkage with the self-sterility alleles than they do from the expected 3 : 1 ratios.

Three families arose from backcrosses of a heterozygous male to a recessive female. In each case, the observed ratio was not even close to a 1 : 1 ratio. All three families appear to arise from crosses in which the *bu* gene is linked with the common self-sterility allele in the male, for in all cases there is a great excess of dominants in the offspring. In families 3225 and 3361, the numbers are small and there are no recessives, but in family 3362, in which the numbers are larger, there are a few recessives, which undoubtedly represent crossovers.

Whenever disturbed ratios appear, an explanation must be sought, and an explanation that has often been suggested is selective fertilization. In a number of cases it has been shown that this is due to a difference in the growth rate of pollen tubes so that tubes of a given genetic constitution will grow more rapidly or more slowly than those whose genetic constitution is somewhat different. Several discussions of various types of genes for differential pollen tube growth have been recorded, (Brieger 1926, Sansome & Philp 1932, Sears 1937), and Mangelsdorf and Jones (1926) have pointed out that genes affecting the rate of pollen tube growth may be of four types: (1) those which reduce growth rate in sporophytic tissue of the same genetic constitution (self-sterility alleles); (2) those which reduce the rate regardless of the genetic constitution of the sporophytic tissue; (3) those which stimulate the rate in sporophytic tissue of the same genetic constitution; and (4) those which stimulate the rate regardless of the genetic constitution of the sporophytic tissue.

If differential pollen tube growth is considered as a possible explanation of disturbed ratios, the various types of pollen tube growth-rate genes must be considered, for the fact that the ratios of non-*buff* to *buff* are in accord with an explanation based on linkage with self-sterility alleles does not, of course, preclude that some other explanation might fit the facts just as well. If pollen tube growth-rate genes are believed to be the cause of these disturbed ratios, it is simpler to assume that the *buff* gene is linked with the self-sterility alleles than to hypothesize an additional set of genes which affect pollen tube growth-rate; still, it may be helpful to consider briefly the possibility of linkage with some other type of gametophyte gene, perhaps similar to the *Ga* gene of Mangelsdorf and Jones. For example, while families 3103, 3104, 3105, and 3106 agree well with the concept of linkage with self-sterility gene with 5 per cent crossing over, they will also agree just as well with a theory based upon linkage of *bu* with gametophyte genes

TABLE 2. Observed ratios of orange (non-buff) to buff in seven families of which the parents possessed no self-sterility allele in common, and the corresponding expected ratios.

In the first four families, each parent was heterozygous for the buff gene. In the other three, one parent was *bu bu*.

Family	Parents	Observed		Expected		Dev. S.E.
		<i>Bu</i>	<i>bu</i>	<i>Bu</i>	<i>bu</i>	
3001	2901(1) × (7)	11	6	12.8	4.2	1.01
3002	2901(1) × (11)	37	18	41.2	13.8	1.30
3003	2901(1) × (15)	61	27	66.0	22.0	1.23
3015	2901(14) × (1)	13	3	12.0	4.0	0.58
3004	2901(7) × (13)	6	4	5.0	5.0	0.63
3006	2901(9) × (10)	9	13	11.0	11.0	0.85
3009	2901(10) × (5)	3	6	4.5	4.5	1.00

such as *Ga* with 5 per cent crossing over, provided that *Ga* is not merely 4.1 times as successful as is *ga*, as Mangelsdorf and Jones found in maize, but that it is completely successful. Such a theory is very similar to that based on linkage with the *s* genes, except that there should be no correlation between families with disturbed ratios and families whose parents had a self-sterility allele in common. Table 2 lists seven families whose parents did not have a common self-sterility allele, and in all these families the non-buff: buff ratios cannot be regarded as disturbed. On the other hand, the seven families listed in table 3 have parents that shared one self-sterility allele, and they do have disturbed ratios. Family 3001 had parents with no common allele, and conforms sufficiently well to a 3:1 ratio, but four of its F<sub>1</sub> descendants had parents with a common allele and definitely showed disturbed ratios. This would indicate linkage with the *s* genes rather than with *Ga* genes.

TABLE 3. Observed ratios of orange (non-buff) to buff in seven families of which the parents possessed a common self-sterility allele, and the corresponding expected ratios based on absence of linkage between the buff gene and the self-sterility alleles and on linkage with five per cent crossing over.

In the first four families, each parent was heterozygous for the buff gene and *Bu* is coupled with the common self-sterility allele in the male. In the other four, the female parent was *bu bu*, and *bu* is coupled with the common *s* allele in the male.

Family	Parents	Observed		Expected					
				If no linkage			If linkage		
		<i>Bu</i>	<i>bu</i>	<i>Bu</i>	<i>bu</i>	Dev. S.E.	<i>Bu</i>	<i>bu</i>	Dev. S.E.
3103	3001(6) × (22)	21	23	33.0	11.0	4.18	23.1	20.9	0.63
3104	3001(22) × (6)	3	3	4.5	1.5	1.42	3.2	2.8	0.16
3105	3001(8) × (22)	10	10	15.0	5.0	2.57	10.5	9.5	0.22
3106	3001(22) × (8)	3	6	6.8	2.2	2.95	4.7	4.3	1.13
3225	3103(1) × (5)	16	0	8.0	8.0	4.00	15.2	0.8	0.92
3361	3103(52) × (4)	7	0	3.5	3.5	2.65	6.6	0.4	0.65
3362	3103(52) × (40)	36	3	19.5	19.5	5.29	37.0	2.0	0.53

As is shown in figure 4, family 3103 might have arisen from the cross  $s^x bu/s^y Bu \times s^y Bu/s^x bu$ . Because of the elimination of the  $s^y$  male gametes, all the male gametes would be  $bu$  except for the few crossovers, and the expected ratio of  $Bu$  to  $bu$  in 3103 would be approximately 1:1, as was the observed ratio. If buff were linked with the  $Ga$  type of gametophyte genes, and the cross were  $Ga Bu/ga bu \times Ga bu/ga Bu$  as shown in figure 4, the expected ratio of family 3103 would still approximate 1:1. This family, therefore, agrees with both theories. When families 3361 and 3362 are considered, it is observed that both resulted from a cross between a buff female and a non-buff male of family 3103. On the basis of linkage with the self-

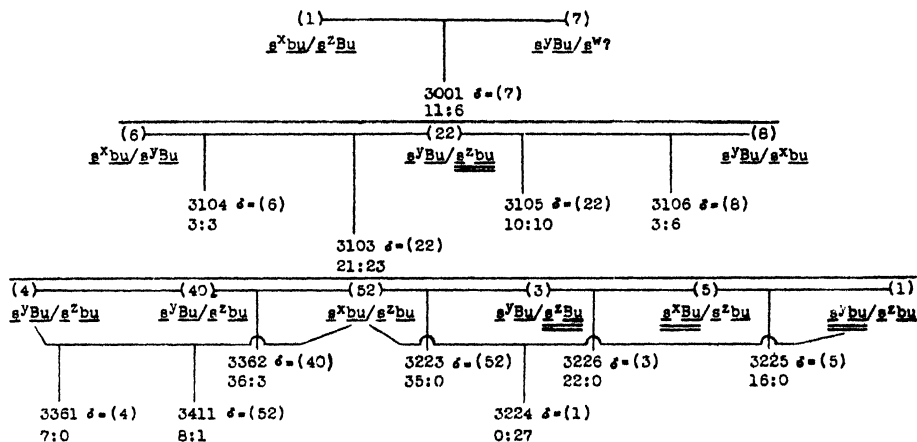


FIG. 4. A pedigree diagram of the families which show linkage between buff and the self-sterility alleles. The ratios beneath the pedigree numbers of the families are the ratios of non-buff to buff. The male parent of each family is indicated, as this is an important consideration when dealing with self-sterility as determined by oppositional genes. Crossover gametes are indicated by a double line beneath the  $s$  and  $bu$  genes of that gamete.

sterility alleles, the buff plant should be  $s^x bu/s^z bu$  and the non-buff plants  $s^y Bu/s^z bu$ . Previous tests (Riley 1935) showed that the self-sterility class of the buff plant was  $s^x s^z$ . The two male plants were not listed in that paper, but they were  $s^y s^z$ . If these non-buff plants are crossed on to the buff female, the  $s^z$  gametes are eliminated in each male as are all the  $bu$  gametes except those that arose by crossing over. The offspring of these two crosses should contain almost entirely non-buff plants. Families 3361 and 3362 conform to that requirement. However, on the other theory, family 3103 should consist of buff plants of the genotypes  $Ga bu/ga bu$  and non-buff plants of the constitution  $Ga Bu/Ga bu$ . If such a non-buff is crossed as a male on to the buff female, approximately half the offspring should be buff, since all the pollen would function. The only way for families 3361 and 3362 to contain

almost entirely non-buff plants but also a small percentage of buffs would be for the male parent of each family to have arisen by a crossover in the male parent of family 3103, so that the constitution of 3103(4) and 3103(40) would be *Ga Bu/ga bu*. The *ga bu* chromosome would be from the female parent, while the *Ga Bu* chromosome would be a crossover chromosome from the male parent. While this is entirely possible, it is unlikely that the only two male parents selected would have both been crossover plants, since the percentage of crossing over is so low. Family 3325 also arose from a cross between a buff female and a non-buff male and contained all non-buff plants. Because of the self-sterility classes of the parents, the parental plants must each have been a crossover plant on the theory of linkage with the self-sterility alleles. On the other theory, the ratio in family 3225 could be obtained only if the male was a crossover identical with 3103(4) and 3103(40). As figure 4 shows, on the theory of linkage with *s* genes, three of the six plants selected for further study must have arisen from one crossover gamete. One would have been a crossover in the male parent of family 3103 and the other two in the female parent. On the other theory, however, four of the six plants would have arisen from crossover gametes, but in all four cases the crossing over would have occurred in the male parent. This is a less likely supposition.

If disturbed ratios are thought to be due to linkage with self-sterility alleles, the real test is the correlation between the morphological character and the self-sterility class. Unfortunately, the evidence for *Nemesia* is not too abundant, but it is consistent. If family 3103 arose from the cross,  $s^*bu/s^*Bu \times s^*Bu/s^*bu$ , the offspring should segregate into .049  $s^*s^*$  non-buff: .451  $s^*s^*$  buff: .476  $s^*s^*$  non-buff: .024  $s^*s^*$  buff. On the other hand, if the genotypes of the parents were  $s^*s^* Ga Bu/ga bu$  and  $s^*s^* Ga bu/ga Bu$ , the offspring should segregate into a ratio of .262  $s^*s^*$  non-buff: .238  $s^*s^*$  buff: .262  $s^*s^*$  non-buff: .238  $s^*s^*$  buff, because the self-sterility classes would be independent of the buff character. Unfortunately, only ten plants were tested for self-sterility classes in this family, and they segregated into an observed ratio of 1:2:5:2. While the numbers were too few to have much statistical meaning, there is a fair agreement between expected and observed buff types and self-sterility classes except that there are too many buffs in the last category. Better results are found in families 3105 and 3106, where a larger number of plants were tested for self-sterility alleles (table 4). Most of these plants were tested in only one direction and by only one pollinator, but both families were expected to split into only two classes, and much more elaborate tests for self-sterility groups in other families showed that if there are only two classes in a family, results are sufficiently accurate even though the plants are tested in only one direction and by only one class. These families add rather important evidence to the hypothesis that the buff gene is linked with the self-sterility alleles with about 5 per cent crossing over.

TABLE 4. Observed ratios of non-buff to buff with the self-sterility classes of the respective families, and corresponding expected ratios assuming (1) linkage between *bu* and the *s* genes with five per cent crossing over and (2) no such linkage but assuming that *bu* is linked with the *Ga* genes. For explanation see text.

Family		<i>s<sup>+</sup>s<sup>+</sup>Bu</i>	<i>s<sup>+</sup>s<sup>+</sup>bu</i>	<i>s<sup>+</sup>s<sup>+</sup>Bu</i>	<i>s<sup>+</sup>s<sup>+</sup>bu</i>	<i>su<sup>+</sup>su<sup>+</sup>Bu</i>	<i>su<sup>+</sup>su<sup>+</sup>bu</i>	$\chi^2$	P (df = 3)
3105	Obs.	....	....	2	9	8	1	.....	.....
	Exp. (1)	.....	.....	1.0	9.0	9.6	0.4	2.17	50-70%
	Exp. (2)	....	....	5.2	4.8	5.2	4.8	10.17	1-2%
3106	Obs.	3	1	0	5	....	....	.....	.....
	Exp. (1)	4.3	0.2	0.4	4.1	....	....	4.19	30-50%
	Exp. (2)	2.4	2.1	2.4	2.1	....	....	7.13	10-20%

Since both buff and pale-upper are recessive genes, some plants may be expected which would be *bubu pp*. Since no such double recessives have been identified in ten families segregating for both buff and pale-upper, even though 110 buff and 82 pale-upper plants have been found, it is highly probable that they cannot be distinguished with certainty from one of the other types and that either *bu* is epistatic to *p* or *p* is epistatic to *bu*. It is easier to test this relationship in families that do not have a self-sterility allele common to both parents, for the segregation of *bu* is greatly influenced by the gametic elimination of the gene which is coupled with the common self-sterility allele in the male. In three of the families in which there is no gametic elimination, the cross was *Bubu Pp*  $\times$  *Bubu pp*. In such a cross, the theoretical ratio is 3 orange (*Bu P*) : 3 pale-upper (*Bu p*) : 2 buff (*bu P* and *bu p*) if *bu* is epistatic, and 3 orange (*Bu P*) : 4 pale-upper (*Bu p* and *bu p*) : 1 buff (*bu P*) if pale-upper is epistatic. The three families that represent this cross segregated into ratios of 4 : 7 : 6, 17 : 20 : 18, and 38 : 23 : 27. In each case, the observed ratio was closer to the expected ratio if buff is epistatic than it is to that expected if pale-upper is epistatic (table 5). One

TABLE 5. Observed ratios of orange : pale upper : buff, and expected ratios (a) if buff is epistatic and (b) if pale upper is epistatic.

(a) If <i>buff</i> is epistatic					(b) If <i>pale upper</i> is epistatic			
Cross = <i>Bubu Pp</i> × <i>Bubu pp</i>								
	<i>Orange</i>	<i>pale upper</i>	<i>buff</i>		<i>Orange</i>	<i>pale upper</i>	<i>buff</i>	
3001 Obs.	4	7	6	$\chi^2 = 1.71$	4	7	6	$\chi^2 = 8.39$
	Exp. 6.4	6.4	4.2	$\bar{P} = 30-50\%$	6.4	8.5	2.1	$\bar{P} = 1-2\%$
3002 Obs.	17	20	18	$\chi^2 = 1.66$	17	20	18	$\chi^2 = 10.34$
	Exp. 20.64	20.64	13.76	$\bar{P} = 30-50\%$	20.64	27.52	6.88	$\bar{P} = \text{less than } 1\%$
3003 Obs.	38	23	27	$\chi^2 = 4.93$	38	23	27	$\chi^2 = 44.05$
	Exp. 33	33	22	$\bar{P} = 5-10\%$	33	44	11	$\bar{P} = \text{less than } 1\%$
Cross = <i>Bubu Pp</i> × <i>bubu Pp</i>								
3006 Obs.	7	2	13	$\chi^2 = 0.75$	7	2	13	$\chi^2 = 5.15$
	Exp. 8.25	2.75	11	$\bar{P} = 50-70\%$	8.25	5.5	8.25	$\bar{P} = 5-10\%$

family arose from the cross *Bubu Pp*  $\times$  *bubu Pp*. The observed ratio was 7 orange:2 pale upper:13 buff; this is much closer to the ratio expected if buff is epistatic (3:1:4) than to that expected if pale-upper is epistatic (3:2:3). It seems probable, therefore, that buff is epistatic to pale-upper and that *bu* and *p* are not linked.

The relationship of orange, buff, and pale-upper is such as is occasionally caused by multiple alleles. This possibility was therefore tested. If there are three alleles such that orange is dominant over buff which is in turn dominant over pale-upper, and if an orange-colored (non-buff, non-pale upper) plant heterozygous for buff is crossed with a pale-upper, all the offspring should be orange or buff, and no plants should be pale-upper. In four families from a cross between an orange and a pale-upper, all three types were recovered. If orange is dominant over pale-upper which is in turn dominant over buff, a cross between two orange-colored plants could not produce all three types. In one family from two orange-colored parents, all three types were recovered. Apparently a two-factor hypothesis with epistasis of buff is more satisfactory than any hypothesis based upon multiple alleles.

There is a small amount of evidence indicating that *o* and *bu* are not linked. Since *bu* is not differentiated from *Bu* in the *oo* plants, the ratio of orange to buff must be used to determine whether there is any linkage. One family segregated into 6 orange:4 buff:15 white and another segregated into 9 orange:13 buff:19 white. In each case the parents were *Oo Bubu*  $\times$  *oo bubu*, and in neither case was the deviation from a 1:1 ratio significant to suggest linkage. It must be remembered, however, that the populations in these families were small.

When orange-colored flowers were placed in hydrochloric acid vapor, the orange color became much paler. It is possible that the paler color in types such as buff and pale-upper may be due to a higher acidity in the cell sap of some of the epidermal cells of the limb in such plants.

**Glass-green (*gl*).** In the glass-green type, the corolla limb varies from Sea-foam Yellow to Pale Glass Green and frequently is so pale as to be almost indistinguishable from white. The tube is orange with or without dark purple spots.

Glass-green behaves as a simple recessive to white. In six instances, two white plants were crossed which must have been heterozygous for glass-green. In one family, the parents were also heterozygous for yellow and for yellow-spot, which complicates the picture, but in the other cases both white and glass-green appeared in the progeny and in four of those families the ratio was approximately 3:1. In the fifth family the ratio was 26:2, but even in this case the deviation divided by the standard error does not greatly exceed 2 and this family can probably be considered as segregating into a 3:1

ratio. In four of the families one self-sterility allele was common to both parents. The close approximation to a 3:1 ratio in these families indicates that glass-green is not linked with the self-sterility alleles. In two families which resulted from reciprocal crosses between two glass-green plants, all the offspring were glass-green. Four families from a cross between a white-flowered plant which must have been homozygous for the allele of glass-green and a glass-green plant contained 132 plants and all were white. It is probable that glass-green is a simple recessive; the gene for this type will be identified by the symbol *gl*.

The relationship between orange and glass-green is indicated by two families. One family arose from a cross between an orange and a white both of which were heterozygous for the anthocyanin gene. The non-anthocyanin offspring segregated into 6 orange non-buff : 4 orange buff : 13 white non-glass-green : 2 white glass-green. It was not possible to distinguish orange glass-green or buff glass-green types from the orange non-glass-green and buff non-glass-green plants, which would indicate that *O* is epistatic to *Gl* and *gl*. That *gl* and *bu* are not one and the same gene which merely exerts a different reaction depending upon whether it is combined with *O* or with *oo* is shown by the fact that the non-buff and buff types are segregating 1:1 while the white and glass-green types are in a ratio of 3:1. Other evidence to support this is the fact that buff is linked with the self-sterility alleles while glass-green is not. The second family came from a cross between orange and white (plus anthocyanin). The non-anthocyanin plants segregated into 9 orange non-buff : 13 orange buff : 10 white non-glass-green : 9 white glass-green. In this family, also, *O* appeared to be epistatic to the *Gl* and *gl* genes, just as *o* appeared epistatic to *Bu* and *bu*. In this family the orange non-buff plants further segregated into a ratio of 7 non-pale-upper : 2 pale-upper. The fact that the white plants of the same family were segregating into 1 non-glass-green : 1 glass-green indicates that pale-upper and glass-green are not the result of one and the same gene acting upon a different background. There is insufficient evidence to show whether *o* and *gl* are linked.

**Yellow** (*y*).<sup>4</sup> There appears to be a type which in many ways resembles buff phenotypically but which appears to be due to a recessive gene acting together with the homozygous *o* gene. Unfortunately, the evidence for the inheritance of this yellow type is not so extensive as might be desired, since yellow in the original material was confused with buff. After tracing buff through several generations, it was realized that it is a modification of orange and is never expressed in an *oo* plant and that the yellow plants were found only in a line that was homozygous for *o*. When it was realized that these two

<sup>4</sup> This symbol should not be confused with the *Y* of a preliminary paper (Riley 1940) which has now been replaced by *O*.

types were genotypically different, it was too late to carry out any further tests, for seeds from the yellow strains were no longer viable.

One family of this original material segregated into 25 non-yellow to six yellow, which would indicate that yellow was recessive. Of the non-yellows, 20 were white and five were glass-green. The segregation into 20 white : 5 glass-green : 6 yellow indicates, although the data are not too numerous, that yellow may be epistatic to glass-green. On this assumption, chi-square for this family equals 0.89. Two families arose as reciprocal crosses between a heterozygote and a yellow and yielded respectively 54 white : 35 yellow and 7 white : 9 yellow. One other family segregated for yellow but will be discussed under the section dealing with the gene for yellow-spot. Apparently yellow is a simple recessive. The symbol for the yellow gene will be *y*.

Linkage between *y* and *o* and between *y* and *gl* has not been tested.

In 1940, a type listed as yellow was purchased and crossed with white. These yellow plants varied in depth of color from Lemon Yellow to almost Glass Green. Whether they represent the old *y* gene cannot be stated at present. Seeds from crosses of these yellow plants were not sown for three years and the only seeds to germinate were from a cross between a pale yellow and a blue. The  $F_1$  plants were white. The non-blue  $F_2$  plants were difficult to classify because the yellows were pale, but the yellow type appeared to be less frequent than the non-yellows. Further tests with this type are being made.

**Yellow-spot (*ys*).** The yellow-spot type is not so well defined in its expression as are some of the other types. The yellow color appears as a large number of dots or streaks radiating out on the lower lip from a small area near the throat (fig. 3). The remainder of the lower lip may be white or Seafoam. The upper lip appears to be entirely white or Seafoam.

In *oo* plants, yellow-spot appears to be recessive to non-yellow-spot, although two families are puzzling. The gene for yellow-spot will be designated *ys*. Ten families resulted from crosses between two heterozygotes, but only seven yielded ratios in which the deviation from a 3 : 1 ratio divided by the standard error was less than two. In one family the ratio was 27 *Ys* : 1 *ys*, resulting in a deviation only 2.62 times the standard error, but in the other two families the ratios were very puzzling, for it appeared as if yellow-spot were dominant. The ratios were 4 *Ys* : 14 *ys* in one family and 2 *Ys* : 7 *ys* in the other. It was thought that perhaps linkage with *s* genes was the explanation, but this does not seem to be the case. In the second family no self-sterility allele was common to the two parents, while in the first there was a common self-sterility allele, but even with such linkage the observed ratio would not be probable and the reciprocal cross gave a fairly good 3 : 1 ratio (16 *Ys* : 3 *ys*). It may be that these two ratios are disturbed because of the difficulty of distinguishing between yellow-spot and non-yellow-spot in



families that have certain combinations of other genes, but there is no evidence that this is so.

One family arose from a cross between two white-flowered plants which were heterozygous for the gene for blue-margin (Riley 1940). This family segregated into 38 white : 54 of a yellow color. The parents of this family are both to be found in a family which is segregating for yellow and for glass-green, and therefore may presumably be heterozygous for *y* and for *gl*. Four sibs of the two parents are heterozygous for the gene for yellow-spot, so presumably the parents of this family might both be *Glgl Yy Ysys*. In that case, the offspring should segregate into a ratio of 27 white to 37 of all the three yellow types. On a white non-blue-margin background, yellow is possibly epistatic to glass-green, but yellow, yellow glass-green, yellow yellow-spot, and yellow glass-green yellow-spot cannot be distinguished from one another, and glass-green and glass-green yellow-spot can be distinguished only with difficulty. In blue-margin plants it is almost impossible to differentiate phenotypically any of these three types with yellow color. In studying this family, then, all the yellowish plants were classed together. On the basis of a three-gene difference and treating the case as one of complementary genes, the expected ratio becomes 39 white : 53 yellowish. The observed ratio fits this hypothesis remarkably well, for the deviation divided by the standard error is only 0.17.

Linkage of *ys* with *o*, *gl*, and *y* has not been tested. Because *bu* and *p* cannot be differentiated on a *oo* background, and because *gl*, *y*, and *ys* cannot be differentiated on a *O* background, any linkage between either *bu* and *p* with *gl*, or *y*, or *p* cannot be determined directly.

**Sectorial Chimaeras.** Lawrence (1931) has pointed out that sectorial chimaeras may sometimes be used to detect recessive genes. These chimaeras may be the result of mitotic abnormalities resulting in somatic nondisjunction. If this occurs in a young bud of a heterozygote, and the chromosome bearing the dominant gene becomes lost, the tissue that develops from it will have only the recessive gene. If this tissue is one that the gene affects directly, it will be phenotypically recessive. Such situations are infrequent in *Nemesia*, but have been encountered occasionally when thousands of flowers were examined.

In one plant of one family from the cross  $OO \times Oo$  and in one of a family that arose from the cross  $OO \times oo$ , a white chimaera was found on an orange-colored flower. Half the plants of the first family and all of the second are *Oo*. The chimaeras therefore were probably the result of the loss of the *O* gene in heterozygotes and confirm the breeding data that orange is dominant over white. One flower of plant 3209(1) had a yellow chimaera on the upper lip of an otherwise white-flowered plant. The parents of 3209 were 3111(4), which is homozygous for *Y*, and 3112(11). Family 3112 was

segregating into 3 white : 1 yellow, so plant 3112(11) might well have been *Yy*. If so, half the plants of 3209 would be *Yy* and presumably plant 3209(1) was one of these plants. This is a further indication that yellow is recessive to white and is different from orange.

#### SUMMARY

Six genes for yellow or orange flowers have been found in *Nemesia strumosa*. The white-flowered type is regarded as the standard.

Gene *O* produces a deep yellow or orange color on both the upper and lower lips of the corolla. The color of *O* plants is usually Cadmium Yellow or Light Cadmium but in a few cases is Orange. Plants with the *O* gene may have the color diluted by two other genes, *bu* and *p*. Gene *p*, pale-upper, lightens the color of the upper lips to approximately Apricot Yellow, while *bu*, buff, changes the upper lips to Sulfur Yellow and the lower lips to Buff Yellow. Both genes show a slight variation from these hues depending probably upon modifying genes. Gene *o* is epistatic to *p* and *bu* which are therefore expressed only in the presence of *O*. Gene *bu* is epistatic to *p*, so that *O-ppbubu* and *O-P-bubu* plants are indistinguishable. Gene *bu* is linked with the self-sterility alleles. All *O-P-Bu-* plants are orange.

Three genes produce some yellow color in *oo* plants but apparently are not expressed in the presence of *O*. Gene *y*, yellow, produces yellow-colored flowers. This is recessive to *Y*, non-yellow, although the behavior appears to be somewhat erratic and the ratios disturbed. The gene for glass-green, *gl*, produces flowers in which the corolla limb is Glass Green or Seafoam Yellow. It is recessive to *Gl*, non-glass green. The yellow-spot gene, *ys*, produces a yellow spot with yellow lines radiating from it on the lower lip of the corolla near the throat. Yellow appears to be epistatic to glass-green and possibly to yellow-spot. Glass-green non-yellow-spot and glass-green yellow-spot plants have not been distinguished and it is not known which is epistatic. Plants with the constitution *oo Y- Gl- Ys-* are white.

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## THE VARIATIONS AND ORIGIN OF *BOTRYCHIUM LANUGINOSUM*<sup>1</sup>

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*Botrychium lanuginosum* Wall. ex Hook. & Grev., a remarkable Asiatic species, is closely related to *B. virginianum* (L.) Sw., but differs in having the fertile spike or segment inserted in a position subject to variation, generally above the level of the two basal pinnae. On the basis of 24 specimens from several American herbaria, a brief article (Chrysler 1925) called attention to the significance of this species from a morphological standpoint. In 1938, a visit to London afforded an opportunity to study the large collections at the British Museum and at Kew. During recent months additional specimens have been made available by the following herbaria:

Amherst College  
Botanical Garden, Buitenzorg, Java  
University of California at Berkeley  
Chicago Natural History Museum  
Cornell University  
Royal Botanic Garden, Edinburgh  
Gray Herbarium, Harvard University

University of Michigan  
Missouri Botanical Garden  
New York Botanical Garden  
Philadelphia Academy of Natural Sciences  
Princeton University  
United States National Museum  
Yale University

It is a pleasure to acknowledge my indebtedness to the curators of these herbaria. All told 217 specimens have been examined, representing all parts of the range of the species, which may be roughly traced thus: N. W. India, Ceylon, New Guinea, Philippines, Tibet. A few of the specimens take the form of photographs, especially that of the type sheet, which Ballard (1940) has located at Edinburgh and with great kindness has photographed for my use. Thanks are due also to Dr. H. H. Bartlett for furnishing information on certain points from his field experience, and for the loan of sheets from his valuable series, No. 6560, illustrating variation. Dr. R. T. Clausen has been good enough to read the manuscript.

### NOMENCLATURE

*Botrychium lanuginosum* first appears as Number 48 in Wallich's *List* (1828), as a *nomen nudum*. Besides the type sheet in Greville's herbarium at the Edinburgh Botanic Garden, consisting of two plants and annotated "48. *Napalia*. E.I.C.," there is at the British Museum a sheet bearing five plants and labelled "Nepal, 1821, Dr. Wallich No. 48"; at Kew a sheet

<sup>1</sup> Publication of Bureau of Biological Research, Rutgers University.

inscribed "Kamoun Wallich 1829. Type number"; a second: "Nepalae 1821 Type number"; a third (in Hooker's collection): "*Osmunda lanuginosa* Wall. *Napalia* 1821" bearing two specimens; at the U. S. National Museum a sheet consisting of one complete plant and bearing a British Museum label inscribed: "*Botrychium lanuginosum* Wall. = *B. virginianum* Sw. Nepal 1821. Wallich 48." How many of these plants were collected by Wallich is open to question. In 1829 Hooker and Greville presented a formal description of the species as explanation of their plate 79, the origin of which from the Edinburgh sheet has been forcibly argued by Ballard (1940). This sheet may hence be considered the type. But it is unfortunately true that over 90 per cent of the plants labelled *B. lanuginosum* which I have examined conform neither to plate 79 nor to the description, although the larger plant of the Edinburgh sheet is an excellent example of what has ordinarily been called *B. lanuginosum*, having the fertile spike inserted above the two basal pinnae, and lacking only the basal part of the *bulbus* bearing lanugo at its apex. Ballard has offered the plausible explanation of the drawing of plate 79 as a combination of the two plants of the Edinburgh sheet. Dr. R. T. Clausen's remark upon seeing the photograph of this sheet was that probably Hooker and Greville considered that the larger plant was abnormal. From the material available to these authors they seem to have had their minds fixed on a plant having the habit of *B. virginianum* (*frondem infra apicem gerens*) but possessing *bulbus ovatus, subsquamosus, apice lanigerus*, and this is exactly what is represented in plate 79. Beddome's (1863) drawing more nearly conforms to current conceptions of the species, representing a leaf in which the fertile spike occupies a position above the fourth pinna. In 1833 Hooker acknowledged that he had had access only to very small specimens, and amended his earlier description thus: "In general the insertion of the scape is above the lower primary division of the frond." Presl adopted the corrected description in his *Supplementum* (1845). Doubts arose as to the distinctness of *B. lanuginosum*, as appears in Moore's *Index* (1857) where it is listed as a variety of *B. virginicum* Willd.: " $\beta$  *lanuginosum* M." To this point of view Milde (1864) objected on the following grounds: (1) the higher level of insertion of the fertile spike, (2) straight form of the epidermal cells *vs.* the flexuose form in *B. virginianum*, (3) catadromy of the secondary branches of the frond *vs.* the anadromy of *B. virginianum*. Milde's monograph (1869) emphasizes the last feature and regards the plant which was represented by Hooker and Greville as a juvenile specimen. Clarke (1880), who had the benefit of field experience, was not impressed by the catadromy as a safe distinction, and considered all of the Himalayan material to be one species. Hope (1903) presents additional observations on this and related questions. He regards *B. lanuginosum* as a distinct species, as do other students of the group, such as Bitter (1900), Christensen (1906), and Clausen (1938).

## ANALYSIS OF THE SPECIMENS

As the foregoing paragraph implies, *B. lanuginosum* is closely related to *B. virginianum*. Hooker and Greville's treatment would clearly indicate such relationship. The specific name would suggest a practical distinction, but it may readily be verified by inspection of a fair-sized series of the latter species that lanugo may be present at the base of the stipe, also to a lesser extent at regions of branching of the leaf. Moreover some specimens of *B. lanuginosum* are almost entirely glabrous, a condition which cannot be attributed altogether to wear. Nakai (1925) has in fact distinguished the variety *leptostachyum*. Lanugo is much more apt to characterize large specimens, where it sometimes clothes the entire stipe. Otherwise Hooker and Greville's characterization, *Bulbus ovatus, sub-squamosus, apice lanigerus*, agrees with later observations. The *bulbus* moreover seems to be an important character; the base of the stipe in *B. virginianum* would not impress one as bulbous, while in *B. lanuginosum* it is definitely swollen. Concerning the anadromous *vs.* catadromous distinction it may be well to recall a remark of Clarke (1880): "the lowest primary pinnae are often twisted in drying." It is easy to demonstrate anadromy in *B. virginianum*, but such observations as I have been able to make on herbarium material of *B. lanuginosum* confirm Clarke's statement that while there is a strong tendency to be catadromous, the secondary pinnae are often nearly opposite and sometimes they are slightly anadromous. The character hence appears to have little value as a practical distinction.

The variations shown by the leaf may be grouped in four "plans," as follows:

(1) The *virginianum* plan, in which the fertile spike is attached (adaxially) at the base of the frond (fig. 1). As clear examples may be cited: University of California No. 588663, collected by R. R. Stewart in Mussoorie (N. W. India); University of Michigan, collected by H. H. Bartlett as No. 7912 in Habinsaran, Sumatra. Both of these show the bulbous enlargement at the base, with a moderate amount of lanugo.

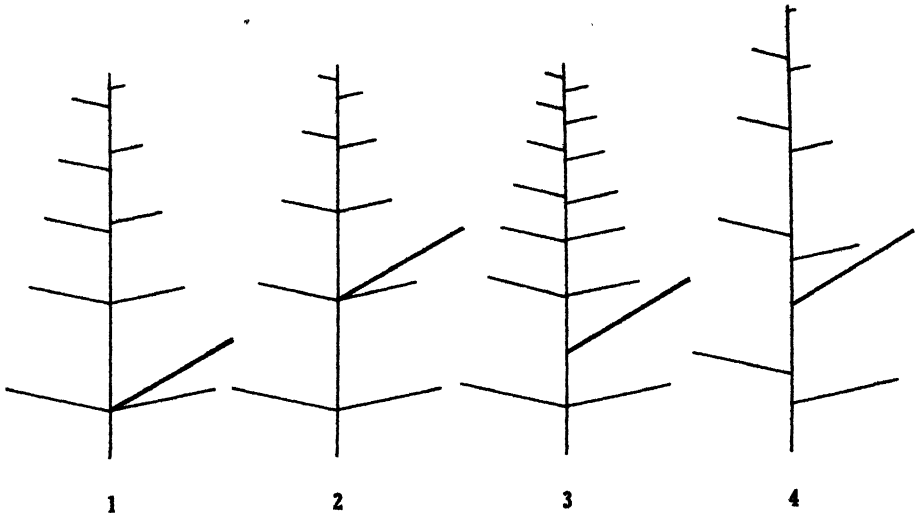
(2) The fertile spike arises in median position accompanying two sterile pinnae which belong to the second node of a leaf rather than to the basal node (fig. 2). This plan may be visualized as a plant of *B. virginianum* having an extra pair of sterile pinnae below the normal "trio" of two sterile pinnae and the fertile spike.

(3) The pinnae are opposite in arrangement except near the apex of the leaf; the fertile spike arises between the nodes formed by the bases of opposite pinnae, generally between the first and second nodes (fig. 3). In a large number of plants it may be distinctly seen that the fertile spike arises adaxially.

(4) The pinnae are strictly alternate throughout the leaf, except that

the alternation is interrupted by the fertile spike, which in about 75 per cent of the plants assigned to this plan is inserted between the second and the third pinna, and may frequently be determined as adaxial even though in pressing it has been bent over to one side (fig. 4).

Over thirty plants lying between plans 3 and 4 present interesting conditions. For instance, a specimen collected in Assam by G. Mann (in the Buitenzorg Herbarium) shows a basal pair of pinnae, followed by the fertile spike which is considered to represent the fusion of two (Chrysler 1910), next by two pinnae arising only 3 mm. apart. Then comes an 18 mm. space followed by two pinnae 3 mm. apart, and so on. Evidently the tendency to



FIGS. 1-4. Diagrams of plans 1-4; for explanation see text.

the opposite plan is present, but fully expressed only in the basal pinnae and the fertile spike. If the prevailing conception of a fern leaf as essentially a scorpioid sympodium is adopted, this leaf exemplifies the exceedingly frequent type in which the apex retains the primitive condition while, as the base is approached, the pinnae become nearly or quite opposite. This condition is common in *B. virginianum* (see also figure 1). Plants of this type occasionally show a zigzag plan, strongly suggestive of a sympodium.

Occasional specimens have been met in which a fertile spike appears to be paired with a sterile pinna. To illustrate this condition sheet No. 1429168, U. S. National Museum, may be cited. Certain other plants are better interpreted as belonging to plan 1. There is no inherent reason why two opposite pinnae, each with a single vascular bundle but one pinna fertile, should not occur as an abnormality, especially in view of the observation of sterile pinnae bearing a few sporangia. Bitter (1900) refers to these plants as "not

rare"; very few such plants have been found in the present study. Hope (1903) describes a plant having a small fertile pinnule on one of the lower pinnae. Another abnormality mentioned by Bitter is the presence of a second, smaller, fertile spike borne on the costa further toward the apex; this condition is very rare in the plants which have come to my attention, and may be exemplified by the British Museum sheet labelled "Ceylon, Gardner 1781. 1846." One of the three plants on this sheet shows an extra fertile spike arising close to pinnae 8 and 9.

In view of the frequency of plants of *B. dissectum* var. *obliquum* (Muhl.) Clute showing forking or paired fertile spikes (Chrysler 1910, 1925), it should be recorded that a single large specimen of *B. lanuginosum* from Pulney Mountains, India, S. B. Fairbanks donor, deposited in the herbarium of Amherst College, shows a spike which 50 mm. from its base divides into two not quite equal branches, each continuing a distance of 80-90 mm.

In my paper of 1925 reference was made to plants with the fertile spike alternating with sterile pinnae and presumably occupying a similar lateral position. This condition was illustrated as figure 1 of the article cited. The figure in question shows the leaf-branches arranged thus: pinna No. 1 L (left); No. 2 R (right); No. 3 is the fertile spike (apparently R); No. 4 L; No. 5 R, continuing in alternate succession to the apex. It should be emphasized that, with the uniform exception of the fertile spike, departures from a strict R, L, R, L, . . . succession are extremely rare in representatives of plan 4. If then the fertile spike of the plant in question represents a single fertile pinna, it should belong to the left side, and number 4 instead of arising on the left side should come from the right side of the axis. If however the fertile spike is interpreted as a fused pair of pinnae, the normal alternation is at once restored. The two interpretations may be represented thus:

(Apparent) : No. 1 L; No. 2 R; No. 3 R (fertile); No. 4 L; No. 5 R; . . .

(Theoretical) : No. 1 L; No. 2 R; No. 3 + 4 (L + R) fertile; No. 5 L; No. 6 R; . . .

The second interpretation brings this specimen into line with plan 4 of an earlier paragraph. Two points of evidence are however lacking: first, the number of vascular bundles in the stalk of the fertile spike; second, signs of twisting which would indicate that the fertile spike is truly adaxial in position. But so many plants in plan 4 have been seen in which the fertile spike is obviously adaxial that a lateral position should be accepted only on sufficient evidence and moreover regarded as extremely exceptional.

The care with which each plant must be examined can not be better shown than in the case of U. S. sheet No. 456830, consisting of a plant collected in Yunnan, China by B. Henry, No. 9213B. At first sight this plant seems to illustrate the alternate arrangement, shifting to opposite beyond the middle of the blade, thus:



No. 1 L; No. 2 fertile; No. 3 L; No. 4 and 5 nearly opp.; No. 6 and 7 nearly opp.; becoming alternate toward the apex. But a lens discloses a slight scar almost opposite No. 1; also nearly opposite No. 3 is a mark where another pinna has apparently been cut off with a sharp instrument. Moreover the fertile spike arises from behind the leaf as it is mounted. The plan should hence be changed to read:

No. 1 L (and 2 R); No. 3 + 4 fertile; No. 5 L (and 6 R); No. 7 and 7, . . . The plant is plainly an example of plan 3.

The four plans which have been distinguished may now be more critically examined. Plan 1 occurs in a very small number of the specimens (about five per cent), and the question at once arises whether they should be assigned to *B. lanuginosum*. They agree well with Hooker and Greville's description and their illustration, but not at all with subsequent treatments of the species. In some of the twelve plants included in this plan the fertile spike and two sterile pinnae do not arise at quite the same level, but the three form a group or trio. The exact insertion is hard to determine because the fertile spike is apt to be markedly decurrent. Not only is this condition evident externally but the vascular strands of the spike descend very gradually through the cortex of the axis before becoming attached to the C-shaped group of petiolar bundles, in contrast to the strands belonging to the sterile pinnae. These strands can sometimes be seen in a pressed specimen, although in critical cases only a series of transverse sections would determine the exact level of attachment of the two sets of bundles. Serial sections through *B. virginianum* show that the spike is attached below the basal pinnae; no material of plan 1 has been available for sectioning. Eight of the plants are small and may be regarded either as depauperate or as young plants. The labels state that two of the plants grew "on rocks," a third "on earth about limestone ledges." But several are medium or large specimens. Of special interest is one of the three plants collected by E. B. Copeland as No. 1848 on Luzon, P. I., and shown in its natural size in figure 5. Two pinnae and the fertile spike arise quite close together, followed by an interval of about 6 mm. distal to which is an almost equal dichotomy. The leaf apparently belongs to a young plant and might be interpreted as a sympodium.

Plan 2 is closely related to plan 3 since in both cases the pinnae are arranged on the opposite plan. Since the exact region of attachment of the fertile spike is open to question as in plan 1, it may well be that certain of the plants listed in plan 2 really belong in plan 3. In fact it is probable that all of them do, on the basis of attachment of the vascular strands, but plan 2 is sufficiently distinguished externally to warrant separation of the 22 plants which have been listed in this group. Of the 68 other plants showing the opposite arrangement (plan 3), 52 have the fertile spike inserted between

the first and second nodes of the leaf, 15 between the second and third nodes, and one between the third and fourth nodes. It has been shown (Chrysler 1925), in the one plant of this group from which serial sections have been prepared, that the vascular supply of the fertile spike arises as two strands, one from each side of the C-shaped bundle system of the rachis; these strands gradually approach the adaxial region and extend upward through the spike. These observations parallel the ones earlier made on *B. virginianum*, and indicate that the spike is a double organ, the equivalent of a pair of leaf-branches, and explain how it comes to have the adaxial position.



FIG. 5. E. B. Copeland's No. 1848; for explanation see text.

Eighty-four plants have been listed as belonging to plan 4; of these 65 resemble the type plant plotted in figure 4, having the fertile spike between pinnae numbers 2 and 3, in the adaxial position and representing a pair of leaf-branches. In five plants the spike arises between pinnae 1 and 2, in eight between pinnae 3 and 4, in five between pinnae 4 and 5, and in one between pinnae 6 and 7. Reference to figure 4 readily shows that the leaf is arranged on the alternate plan only when the fertile spike is counted as two fused pinnae. The figure also brings out the unequal internodes, short ones alternating with longer ones. The prevalence of this condition indicates that the leaf in this species is well on the way to the opposite arrangement of pinnae. It will be noticed that in plan 4 as well as plan 3 the great majority (76-77 per cent) of the plants have the fertile spike situated above the second pinna.

The readiness with which most specimens may be classed as of the alternate or the opposite plan suggests that two varieties or species may be represented. In order to test whether such supposition has any geographical basis, the distribution of 160 plants for which the place of collection is definitely stated on the label has been plotted on an outline map. Almost all of the collections have been made either in the Himalayan region of India and adjacent China, or in a southern belt including the Nilgiri Hill region of India, Ceylon, and East Indies (an isolated group of stations in Luzon, P. I., has been omitted). The tally stands thus:

Northern belt—49 alternate, 40 opposite

Southern belt—19 alternate, 52 opposite

There is hence no clear geographic segregation. The best that can be said for the case is that in the southern part of the range there appears to be a tendency for the opposite arrangement to prevail. Moreover, eleven plants, included in H. H. Bartlett's number 6560, collected on Deleng Piso-piso, Sumatra, present examples of both opposite and alternate forms. As an extreme case may be cited a sheet at Kew: "Herb. J. S. Gamble, Mysore District no. 3087," bearing two leaves growing from the same base, one being opposite in plan and the other alternate! Further, the plants intermediate between plans 3 and 4 offer difficulties. If however the alternate plan is regarded as standing closer to the ancestral leaf-pattern, the predominance of alternate individuals in the Himalayan region compared with the southern belt agrees well with the opinion of Butters (1917): "*Botrychium virginianum* and its allies have a typical boreal distribution and all the tropical forms of this group have evidently come from the north." In this connection it may be well to recall that there is in South Africa a single species, *B. chamaeconium* Bitt. et Hieron. With great kindness Mr. Ballard has furnished me with a photograph of the type specimen; this clearly shows a plant of the opposite plan.

#### PHYLOGENY

The position of the fertile spike in *Botrychium* looks like a case of "phylogenetic slide." But the direction of sliding is not yet certain. There are three possibilities:

1. *B. lanuginosum* is a primitive, still plastic species. Earlier in this study the apparently lateral origin of the fertile spike and its variable position along the leaf-axis suggested that this species had not settled down to the condition which occurs in *B. virginianum* et al. Familiarity with a much larger amount of material leads to the conclusion that laterally inserted spikes are extremely rare, while adaxially inserted spikes, some with visibly double vascular supply, are plentifully represented, even in plants where the sterile pinnae are alternately arranged. Examples of a fertile

spike paired with a sterile pinna also are exceedingly rare if not indeed capable of a different interpretation. In this inquiry the anatomist is hampered by inability to study serial sections of critical specimens. These considerations suggest that the fusion of two leaf-branches to form a fertile spike originated at a date prior to the "wandering" of the spike from one level to another. Hence the second possibility.

2. *B. lanuginosum* represents a youthful species, still in the plastic condition, which has arisen from the *virginianum* type (not necessarily from *B. virginianum*), perhaps in connection with migration from north temperate regions to the moist tropics. It should be noted that the largest plants of any species of *Botrychium* are found in *B. lanuginosum*, some spreading over two herbarium sheets, e.g., a specimen at Yale University, collected in Ceylon by G. Wall (see also Bitter 1900, Hope 1903). By "plastic" is here meant the variability in extent of the phylogenetic slide, with a tendency for the spike to settle down in the position above the first two pinnae. It may be that the decurrent feature of the spike is an indication of an upward slide, although it may also be interpreted as an accompaniment of the upright position of the spike *versus* the dorsiventral habit of the photosynthetic parts of the plant. The small specimens having the *virginianum* plan would represent juvenile plants, according to the second view. Moreover, Clausen's (1938) opinion that *Sceptridium* represents the most primitive division of the genus would suggest that the fusion of sterile and fertile parts began far down on the shoot axis and has moved progressively toward the apex. Again, the imperfect shift from the anadromous to the catadromous condition is in accord with the advanced position given to *B. lanuginosum* in this second possibility.

3. There is finally the stimulating proposal of Zimmermann (1930) and Bower (1935) that the division of the *Botrychium* leaf into fertile and sterile branches represents an ancient antero-posterior dichotomy. Without attempting at present to discuss this "possibility" it may be remarked that it obviously implies a very advanced position for *B. lanuginosum*.

#### SUMMARY

An attempt is here made to analyze the plans presented by the extremely variable *Botrychium lanuginosum*. On the basis of the position of attachment of the fertile spike, and the opposite *vs.* alternate arrangement of the pinnae, the specimens, numbering 217 and representing the known range of the species, are placed in four groups. The analysis suggests that there has been a phylogenetic slide of the fertile spike, probably in the distal direction. If this view is adopted, the species must be regarded as an advanced, still unstable member of the family.

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## THE DISCOVERY AND DISTRIBUTION OF *CINCHONA* *PITAYENSIS* IN ECUADOR<sup>1</sup>

WILLIAM CAMPBELL STEERE

The United States faced a dangerous shortage of quinine early in 1942, when the Dutch East Indies passed into the hands of the Japanese. In an effort to find new supplies of this essential antimalarial drug, the Board of Economic Warfare established *Cinchona* Missions in the several South American republics which had once been the only source of quinine. However, the exploitation of wild *Cinchona* barks had always been an uncertain and hazardous business, and could not compete at all with easily-harvested plantation barks of much better quality. Consequently, as the plantations of Java and Sumatra came to produce ninety-five per cent of the world's quinine supply, wild barks from South America practically disappeared from the market. The problem of reviving this extinct industry had to be solved by botanists, since *Cinchona* trees must be found and identified before procurement of bark could even start.

In the fall of 1942, Dr. F. Raymond Fosberg and I were sent to Colombia by the Board of Economic Warfare, to start the first *Cinchona* surveys at once. We were able to localize substantial quantities of *Cinchona officinalis* and *C. pubescens*, as well as *Remijia pedunculata* (Steere 1945a). However, in March, 1943, we were unusually fortunate in our rediscovery of *Cinchona pitayensis* in the Cordillera Central of southern Colombia, in the Department of Cauca. The type locality of this species, which was supposed to have a rather restricted geographical range, is the village of Pitayó, on the slopes of the Nevado del Huila, north of Popayán. Karsten (1858) made further collections on the slopes of the Colombian volcanos of Cumbal and Chiles, in the Department of Nariño, but no other early collections are known. Even though it was little known to botanists, *Cinchona pitayensis* was of very considerable commercial and pharmaceutical importance just about a century ago. The supply was apparently soon exhausted, however, and the species became so rare that it was nearly forgotten. At the time of our surveys it had been left to reestablish itself for several decades, and we found that it occurred not only in a much greater quantity than we had anticipated, but also over a much wider area.

As Karsten had collected *Cinchona pitayensis* on the Colombian side of the Volcán de Chiles, which is exactly on the Colombian-Ecuadorian frontier,

<sup>1</sup> Paper from the Department of Botany and the Herbarium of the University of Michigan.

an extension of the geographic range of this species into Ecuador could be predicted with some certainty, although it had apparently never been collected there, and is not mentioned in any of the classic works on Ecuadorian botany which treat the Rubiaceae (Jameson 1865; Standley 1931; Diels 1937).

A Cinchona Mission was finally established in Ecuador during the late spring of 1943, and I transferred my field surveys there from Colombia in July, 1943, in order to explore the northern provinces, where no *Cinchona* species were known. The northernmost province, Carchi, was the most logical point to begin the search for *Cinchona pitayensis*, and the provincial capital of Tulcán made an appropriate center of operations. The first survey was made east from Tulcán, over the Cordillera Oriental, in the valley of the Río Chingual. Although *Cinchona officinalis* was discovered for the first time in northern Ecuador, no *C. pitayensis* was found. My second exploration trip in Ecuador was made west from Tulcán, by way of the frontier village of Tufiño. The trail runs somewhat southwest from Tufiño and crosses the Cordillera Occidental on the south shoulder of the Volcán de Chiles by way of a pass at 4500 m. altitude. West of this pass, on the southwestern slopes of Chiles, I found several large stands or "manchas" of *Cinchona pitayensis* (Steere 8043, 22 August 1943). Residents of Carchi told me that *Cinchona* bark or "cascarilla" from such high altitudes could not possibly be of any value, as their good bark all came from Maldonado, farther down the same trail, at an altitude of 1500 m. or lower. However, they were finally convinced that this bark might have some value—it is extremely bitter in the field—and agreed to search for more manchas on other ridges in the same region.

After the original discovery of *Cinchona pitayensis* in Ecuador, many other surveys were made to determine its geographical distribution in the country. Large amounts were found almost at once all along the western slopes of the Cordillera Occidental between the Colombian frontier and the Río Mira, in the Province of Carchi. The largest quantities were found west of El Angel, and still farther west, on the slopes of the isolated Cerro Golondrinas. *Cinchona pitayensis* also exists in the Cordillera Oriental of Carchi, in the region of Huaca. With a survey party, I crossed this range south of Huaca, by way of the enormous Hacienda Indúgel, reaching the headwaters of the Río Cofanes, in the Oriente. Some trees were found on both sides of the eastern range, but no large manchas which would justify exploiting this almost inaccessible region (east side, Steere 8125, 22 October 1943; west side, Steere 8153, 27 October 1943).

At first, I had the idea that *Cinchona pitayensis* would be found only in Carchi, the northernmost province of Ecuador, at least in the western Andes. This supposition was based on the phytogeographical fact that the "fraile-

jón," *Espeletia Hartwegiana*, which is a common and conspicuous element of the Colombian páramos, and forms the dominant high-páramo vegetation in Carchi, does not extend farther south in Ecuador than the Río Mira. Many other elements of the southern Colombian flora are also restricted in Ecuador to the Province of Carchi. Since *Cinchona pitayensis* occurs not far below the páramo, between altitudes of 2500 and 3200 m., I had assumed that it, likewise, would have its southward distribution limited by the deep, desert valley of the Chota and Mira rivers. Therefore, the discovery of substantial quantities of it in Imbabura Province, south of the Río Mira, had considerable botanical significance as well as economic importance. My first survey in Imbabura was made late in November, on the southwest slope of Volcán de Cotacachi, west of Otavalo, in the company of W. B. Drew and F. M. Ownbey. Along an old trail to Intag, through a region called Selva Alegre (for some unknown reason!), substantial quantities of *Cinchona pitayensis* were found (Steere 8191, 3 December 1943). Later in December, working alone, I explored the Colonia Buenos Aires, just south of the Río Mira, northwest of the Volcán de Cotacachi, and found that the zone between 2500 m. and 3000 m., as in other regions, contained abundant *C. pitayensis* (Steere 8201, 15 December 1943). Later surveys in Imbabura by other botanists of the Cinchona Mission, especially by W. B. Drew, demonstrated that the band of *C. pitayensis* extends from the Río Mira south to the Río Guayllabamba, at appropriate altitudes, thus reaching the northernmost part of the Province of Pichincha.

In May, 1944, *Cinchona pitayensis* was discovered on the western slopes of the Volcán de Pichincha, very near Quito. This important discovery resulted from a field observation of plant associations, and demonstrates clearly the value of our study of associated plants, especially members of the Rubiaceae (Steere 1945b). In the zone of the Río Plata, in northernmost Carchi Province, where *Cinchona pitayensis* was first found, an associated plant was *Cephaelis Jamesonii* Standl., another member of the Rubiaceae (Steere 8039, 22 August 1943; Steere 8093, 6 October 1943). This fact in itself had no significance until many different stands of the *Cinchona* had been discovered in the provinces of Carchi and Imbabura, and it was noted each time that the *Cephaelis* was always present in the same altitudinal zone (Imbabura: Steere 8203, 15 December 1943). Since the original specimen, upon which Standley (1931) based *Cephaelis Jamesonii*, was collected by Jameson "in declivitate occidentali montis Pichincha, alt. 2400 meters," it was considered worth while to search for *Cinchona pitayensis* there, in view of the common association of these two species in the more northern provinces. Consequently, a trustworthy field assistant and "conocedor," Antonio Romo, who had worked with me in Carchi and Imbabura, and who knew *Cinchona pitayensis* in the field, was entrusted with an independent



search for it on the west side of Pichincha. He worked south from Calacalí, and on May 24, on the Cerro de Campana, he found the first *C. pitayensis* collected south of the equator, a convincing corroboration of the theory outlined above. Since then, further survey work has shown a considerable quantity of this high-yielding species to exist on the slopes of Pichincha.

The discovery of *Cinchona pitayensis* on Pichincha demonstrated that this species had been able to migrate southward beyond a second phyto-geographical barrier, the deep, desert valley of the Río Guayllabamba, and that it should occur still farther south. Consequently, further explorations were gotten under way at once in the western Andes between the volcanos Iliniza and El Corazón. *Cinchona pitayensis* was soon found to be abundant in the Province of León; north of Pilaló by G. W. Prescott, and in the region of Sigchos by M. Acosta-Solis. A curious feature of the species in León Province is that although its morphological character and its habitat preference are quite typical, its bark is not particularly rich in alkaloids, especially quinine. The cause of this unusual condition will probably be found in some soil factor, although the species itself may be more variable at the edge of its geographic range.

We continually heard rumors that a good quality of *Cinchona* was harvested by Colombians, in the last century, on the eastern slopes of the great mountain mass of Cayambe, in the Eastern Andes. In the hope that a new area of *Cinchona pitayensis* might be discovered, W. B. Drew, Ira L. Wiggins, and G. W. Prescott carried on extensive explorations under the most arduous and difficult field conditions imaginable, but without success. Nevertheless, this species probably does extend still farther south in both ranges of the Andes. The exploratory work, and any work of exploitation which may follow it, will always be made difficult by several factors, especially the cold, wet climate preferred by *Cinchona pitayensis*, the extreme ruggedness of the country and the consequent lack of trails between 2500 m. and 3500 m., and the unwillingness of the people to believe that high-yielding cascarilla can be obtained at such high altitudes (Steere 1944).

*Cinchona pitayensis* was proposed in 1849 by Weddell, not as a new species, but as a new name to replace *C. lanceolata* Benth. (1845), pre-occupied by *C. lanceolata* Ruiz & Pavón (1799). Weddell chose the specific name "pitayensis" because the type specimen came from the region of Pitayó, as already mentioned. In Colombia, this species may form large trees, up to a meter in diameter (Karsten 1858; Standley 1930), and I have seen trees 80 cm. in diameter above Tacueyó, not far from the type locality. In Ecuador, the trees are smaller, and of hundreds of trees which I have seen, none had a trunk over 50 cm. in diameter, with an average of perhaps 35 cm. Furthermore, the leaves are more pubescent, especially when young, and the capsules are less strongly ribbed. The Ecuadorian form was pro-

posed as a new species, *Cinchona corymbosa*, by Karsten (1858), on the basis of specimens from southernmost Colombia. Although this name has generally been treated as a synonym of *C. pitayensis* (Standley 1930), there appears to me to be some reason to keep them separate, perhaps with varietal rank, especially after having seen both forms in the field. The abundant herbarium material which has been collected in Colombia and Ecuador during the past two years will eventually provide a definite answer to this problem, when the specimens can be gotten together for botanical study.

The form of *Cinchona pitayensis* which we now know to occur in the four northern Andean provinces of Ecuador is a beautiful tree with straight, unbranched trunk, which is clear white above and brown below. The white coloration, which is especially conspicuous in dry situations, apparently results from a growth of lichens. When the bark dries, it shows characteristic transverse fissures, especially bark from the upper part of the trunk. Because of its high alkaloid content, of which about half is quinine, the bark is very bitter with the peculiar taste of quinine, either fresh or dry. There are other members of the Rubiaceae which grow with *Cinchona pitayensis* and might be confused with it, but the very bitter bark of the *Cinchona* easily distinguishes it from other members of the family which occur at the same altitude. The rather slender trunk averages 30–35 cm. in diameter in mature trees, at breast height, and a tree of this size will give about 130 pounds of wet bark, if branches down to 6–7 cm. in diameter are stripped. Since the bark of *C. pitayensis* contains less water, on a percentage basis, than the bark of *C. pubescens*, we estimated in our survey work that three trees would produce one hundredweight of dry bark. The trunk does not branch until the crown is reached, and then suddenly breaks up into a complex system of stiff branches. The crown is conspicuously rounded, or often somewhat flat-topped. The leathery leaves are rather stiffly erect-spreading, clustered at the tips of the twigs, with a very characteristic aspect. When young they are a clear, dark green, and very glossy above. Some of the old leaves, especially when exposed to sunlight, become a bright scarlet before they fall off. When one examines the top of the forest from above or on the opposite side of a steep valley, this species can be recognized for a considerable distance by the rounded crowns, the deep green color and glossiness of the leaves, as well as their peculiar arrangement and the occasional scarlet old leaves. The trees usually occur in diffuse groups or manchas of 5–50, and are often more or less of the same size and age within the group. *Cinchona pitayensis* nearly always grows on very steep slopes, in regions with a heavy rainfall, and at altitudes between 2500 and 3230 m. Nearly every region in which this species occurs is decidedly volcanic, and it seems to reach its greatest abundance on the actual slopes of volcanos, from the Nevado del Huila in Colombia to El

Corazón in Ecuador. This species seems to inhabit only virgin forests and does not reappear if the forest is cut or burned, at least for a long time. The habit of *Cinchona pubescens* is very different, as it can colonize river bottoms, pasture fields, and abandoned clearings with the greatest facility.

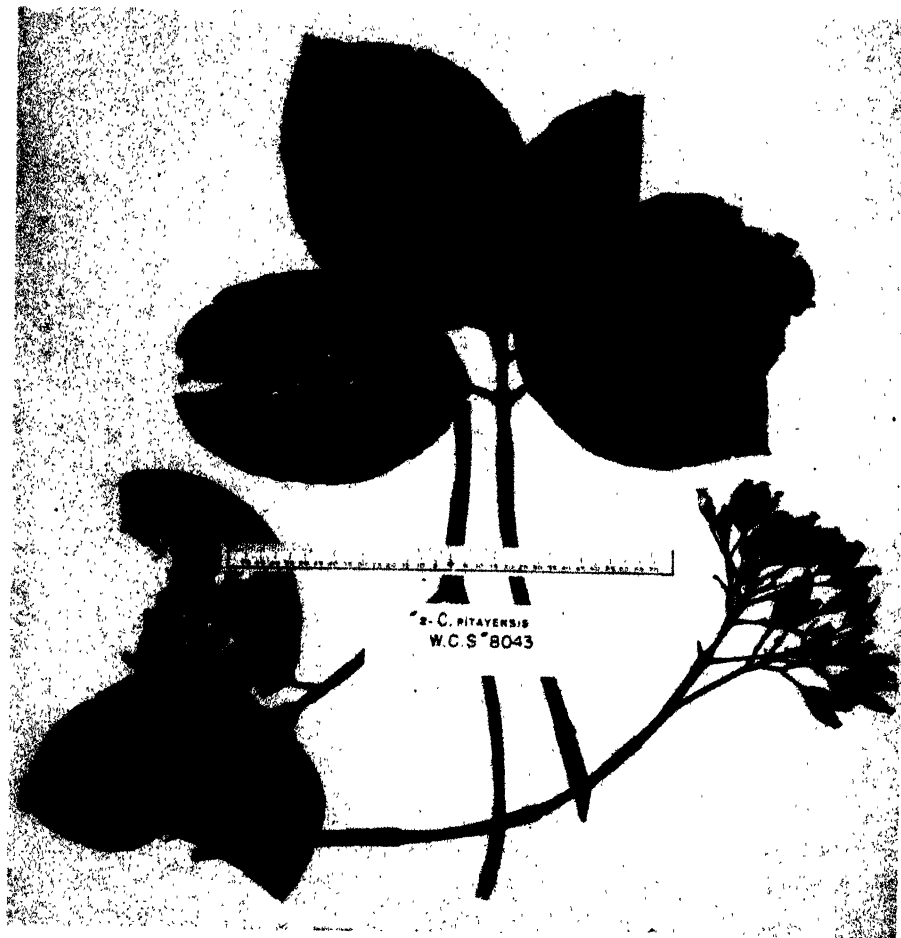


FIG. 1. *Cinchona pitayensis*, leaves and capsules. In this species some capsules dehisce at the base, and others at the apex. Photograph by courtesy of the Corporación Ecuatoriana de Fomento.

The flowers of *Cinchona pitayensis* in Ecuador are brownish-purple to purple and have a strong fragrance of vanilla (coumarin). The inflorescence is very compact, and usually flat-topped, very different from the diffuse, elongated inflorescences of *C. officinalis* and *C. pubescens*. In the latter species, an inflorescence may reach a meter in length. The fruits, likewise, are in a compact, flat-topped cluster, and present a contradictory

condition in the genus *Cinchona*, since about as many of them open at the top and split downward as open at the bottom and split upward (fig. 1). Thus, in the same cluster of fruits one finds capsules opening in the typical *Cinchona* manner and others opening in the manner of *Remijia* or *Ladenbergia*. However, in view of the typical *Cinchona* flowers, and the high alkaloid content of the bark, as well as the group of alkaloids represented, there can be no doubt about the generic position of this species.

The vegetation of the *Cinchona pitayensis* forest is the typically luxuriant growth of a high altitude, broad-leaf rain forest. A commonly associated plant in the Cordillera Occidental is a climbing bamboo (*Chusquea scandens*), and in the Cordillera Oriental may be an enormous, broad-leaved grass (unidentified), locally called "chamizo." As already mentioned, a very useful indicator plant of proper altitude and habitat conditions for *Cinchona pitayensis* is *Cephaelis Jamesonii*.

Soon after its original discovery in Colombia, *Cinchona pitayensis* was found to have the highest-yielding bark of any species in the country, not only in total alkaloids but also in quinine, and large quantities were harvested and exported under the name "quina de Pitayó." In the zone of Tacueyó, near the type locality on the west slope of the Nevado del Huila, the bark averages six per cent of total crystallizable alkaloids and three per cent of quinine sulfate. One of my samples gave the extraordinarily high analysis (for a wild bark) of 5.3 per cent of quinine sulfate and 8.1 per cent of total crystallizable alkaloids. In Ecuador, the alkaloid content of this bark does not seem to be so high as in the northern part of its geographic range, in Colombia, and it apparently becomes progressively less rich in alkaloids toward the south. The highest analysis I have seen for an Ecuadorian sample has been 7 per cent of total crystallizable alkaloids and very little over 4 per cent of quinine sulfate, whereas the average content is about 5 per cent of alkaloids and 2.5 per cent of quinine sulfate. Although this may not be quite as high as the alkaloid content of another form of *Cinchona pitayensis* in parts of Colombia, it still is the highest yield of any species in Ecuador, and is especially important because of its high consistency. An additional advantage of *Cinchona pitayensis* over the other Ecuadorian (and Colombian) species is that it produces the rare alkaloid quinidine in small but appreciable quantities (to 1 per cent). Quinidine is an essential drug for the treatment of certain heart diseases and does not exist as more than traces in any other *Cinchona* species of the northern Andes.

There is a strong and widespread feeling among Ecuadorian cascarilla producers that barks from lower altitudes are apt to be of a higher quality than barks from high altitudes. There is a certain amount of botanical evidence to support this idea, and it is obvious that plants will grow faster in the tropics at lower altitudes, other conditions remaining equal, because

of the increase in temperature. For example, in the western Andes, in the Province of Bolívar, the "serrana" variety of *Cinchona pubescens*, typical of high altitudes, contains an average of perhaps 3 per cent of pure cinchonine, without quinine or other alkaloids, whereas the "roja" variety of the same species, at much lower altitudes, produces bark with 4-5 per cent of total crystallizable alkaloids and 1-2 per cent of quinine sulfate. In the Eastern Andes, the variety of *Cinchona officinalis* which occurs in the valley of the Río Pastaza between 1200 m. and 1500 m. produces bark with an average of four per cent of total crystallizable alkaloids and one per cent of quinine sulfate. On the other hand, the variety which occurs at about 2000 m. produces bark with less than two per cent of total alkaloids and no quinine, so that it is economically worthless. One of the most interesting experiments that could be performed in Ecuador would be to plant seedlings or cuttings of *Cinchona pitayensis* of a high-yielding clone at different altitudes, in order to see if the quinine sulfate content could be increased by altering the climatic factors. Under any circumstance, this species is one of the many rich botanical resources of Ecuador, and is worthy of extensive experimental study, which will undoubtedly result in the development of valuable cultivated varieties.

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## SOME MELASTOMACEAE OF COLOMBIA

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The recent intensive collecting of Dr. José Cuatrecasas in various parts of Colombia has yielded many interesting species of Melastomaceae, including several novelties and several others hitherto unknown to Colombia, at least so far as my records indicate. Those in the genera *Blakea* and *Topobea* have already been discussed in a separate paper.

Excluding these two genera, 93 species have been identified, of which 15 appear to be undescribed. This would be a very high proportion if the plants had come from the Andes. Most of them were collected in the coastal region of El Valle, which has been neglected by most botanical explorers and which yielded numerous new species to Triana many years ago. Several of his plants were re-collected, probably for the first time. There are still a number of specimens unidentified, chiefly because of lack of flowers, without which genera of this family can seldom be determined with assurance. Among them there appear to be the little known *Miconia caelata* (Bonpl.) DC., a new *Miconia* related to *M. parvifolia* Cogn., a new *Henriettella*, and probably some other undescribed species.

**Ptilanthus** Gleason, gen. nov. Hypanthium hemisphaericum anguste 5-alatum, inter alas 5-nervium. Calycis tubus non productus; sepala triangularia secus medium alata, dentibus exterioribus nullis. Petala lanceolata angustissime acuminata. Stamina 10 isomorpha; antherae subulatae poro terminali dehiscentes; connectivum infra thecas brevissime productum ex-appendiculatum. Ovarium multiovulatum liberum summo tomentulosum; stylus rectus gracilis; stigma punctiforme. Inflorescentia terminalis paniculiformis.

**Ptilanthus scandens** Gleason, sp. nov. Liana magna, ramis ultimis subteretibus arcte furfuraceis. Petioli graciles, 2-4 cm. longi, dense brunneo-furfuracei. Laminae herbaceae, late ovatae, 8-14 cm. longae 6-10 cm. latae, apice subiter contractae in apiculum obtusum 1-2 cm. longum, basi leviter cordatae lobis paulo productis et saepe revolutis, supra glabrae, subtus ad venas furfuraceae ad paginam minutissime brunneo-punctatae, 5-pli-nerviae jugo uno marginali altero submarginali neglecto. Cyma paniculiformis terminalis ca. 5 cm. longa. Flores 5-meri brevissime (usque 1 mm.) pedicellati. Hypanthium glabrum 2.2 mm. longum. Sepala 0.9 mm. longa acuta. Petala alba 6 mm. longa, longe acuminata. Filamenta complanata 2.2 mm. longa; antherae 2.6 mm. longae, poro ventro-terminali dehiscentes. Ovarium 3-loculare; stylus 3 mm. longus.

TYPE: *Cuatrecasas 15807*, from the Pacific coast of El Valle, Colombia, alt. 5-50 m. Since fruit is lacking, it is impossible to decide to which tribe of the Melastomaceae the plant belongs. It is a fact that a superior ovary,

such as our plant exhibits, is usually followed by a capsular fruit and an inferior ovary by a baccate fruit, but there are exceptions in both cases. Every character enumerated in the generic characterization can be duplicated separately in some other genus, but the combination of all gives this plant a structure not matched in any genus of the family, so far as it is known to me.

***Calyptrella littoralis*** Gleason, sp. nov. Liana, teste cl. Cuatrecasas. Caules minores dense lepidoto-furfuracei demum glabrescentes. Petioli 8–15 mm. longi. Laminae subcoriaceae, ovato-oblongae vel ovato-lanceolatae, usque ad 10.5 cm. longae 5 cm. latae, caudato-acuminatae ad apicem obtusum, integrae, basi rotundatae vel leviter cordulatae, 5-nerviae jugo exteriore submarginali, supra primum minutissime lepidotae, utrinque densiuscule resinoso-punctatae. Panicula terminalis pauci-ramosa 6 cm. longa furfuracea. Flores 4-meri in capitulis paucifloris ramulos terminantes. Hypanthium poculiforme, 3.5 mm. longum, arcute minuteque lepidotum. Calyx calyptriformis lepidotus ad torum deciduus. Petala alba obovata acuta 4 mm. longa. Stamina isomorpha; filamenta 2.6 mm. longa; antherae linearisubulatae, poro ventro-terminali dehiscentes, thecis convolutis 2.6 mm. longis; connectivum non elevatum, infra thecas 2 mm. productum quasimodo *Graffenrieda*. Ovarium superum, 2(?)-loculare; stylus 4 mm. longus; stigma punctiforme.

TYPE: *Cuatrecasas* 17698, collected at Quebrada de Guapecito, alt. 0–5 m., on the coast of El Valle. A typical *Calyptrella* in every respect except its climbing habit. Three other 4-merous species of the genus have been described, of which *C. robusta* Cogn. has large 7-nerved leaves, *C. tristis* Triana has coriaceous leaves obtuse or acute at base, and *C. gracilis* Triana has thin leaves cuneate at base. The two latter species have much smaller flowers than *C. littoralis* and lack the resin-dots on the leaves. All three grow at fairly high elevations in the Andes.

***Conostegia rubiginosa*** Gleason, sp. nov. Arbor. Caules, petioli, venae subtus, inflorescentia, et hypanthia dense rubiginoso-tomentosa, pilis crassis barbellatis et partim stellatis. Petioli 1–2 cm. longi. Laminae subcoriaceae, anguste obovato-oblongae, usque ad 20 cm. longae 9 cm. latae, abrupte caudato-acuminatae, acumine 1–2 cm. longo, integrae, basi obtusae, 5-nerviae vel sub-5-pli-nerviae, supra glabrae opacae, subtus stellato-pubescentes, supra venis planis secundariis obscuris, subtus venis omnibus valde prominentibus. Inflorescentia ca. 10 cm. longa. Alabastra acuta, obovoidea, 10 mm. longa. Hypanthium hemisphaericum, ca. 5 mm. longum. Petala alba, late triangulari-obovata, 9 mm. longa, fere totidem lata, multinervia, uno latere erosa. Stamina 24 isomorpha. Filamenta 3.3–3.5 mm. longa. Antherae oblongae, obtusae, 2.7 mm. longae, thecis infra filamentum breviter productis; connectivum simplex. Stylus teres, 5.6 mm. longus; stigma capitatum, fere 1 mm. latum.

TYPE: *Cuatrecasas* 17700, collected at Quebrada de Guapecito, Pacific coast of El Valle, alt. 0–5 m.; also 17538, from the same region. The species differs from other Colombian representatives of the genus in its densely tomentose stems and inflorescence.

***Conostegia Cuatrecasii*** Gleason, sp. nov. Frutex vel arbor parva usque ad 4 m. alta. Caules, petioli, rami quadrangulati, et inflorescentiae tenuiter

stellato-furfuracea. Petioli usque ad 4 cm. longi. Laminae tenuēs, ellipticae, usque ad 24 cm. longae 11 cm. latae, abrupte angustatae in apiculum obtusum ca. 1 cm. longum, basi acutae, obtusae vel subrotundae, 5-nerviæ, supra glabrae nitentes, subtus glabrae opacae. Panicula pyramidalis, longe pedunculata, 5-13 cm. longa. Alabastra obovoidea, 8-9 mm. longa, acuta, breviter apiculata, glabra, rugulosa. Flores 6-meri. Hypanthium hemisphaericum, 3.7 mm. longum. Petala alba vel rosea, valde inequilatera, obovata, 9-10 mm. longa. Stamina isomorpha. Filamenta loricata 5 mm. longa. Antherae oblongae, obtusae, 3.5-4 mm. longae, poro terminali dehiscentes, 4-loculares; thecis cum connectivo infra apicem filamenti breviter productis in lobos 2 rotundatos. Ovarium inferum, 6-loculare. Stylus 5.5 mm. longus, superne paullo dilatatus; stigma capitatum, 1.3 mm. latum.

TYPE: *Cuatrecasas 17612*, collected on the Río Cajambre, coast of El Valle, alt. 5-80 m.; other specimens collected by him in the same general locality are *14386*, *17001*, *17273*, and *15142*, the latter at an altitude of 900-1180 m. Another sheet is *Killip 11805*, from the Río Dagua, which, according to my notes of 1928, is the same as *Triana 3942*. It is closely related to *C. Poeppigii* Cogn., in which the buds are only 7 mm. long or less, the petals pink, 6 mm. long and proportionately much wider, the stamens smaller, and the style shorter.

***Miconia calcarata*** Gleason, sp. nov. Arbor grandis, ramis ultimis teretibus obscure brunneo-furfuraceis mox glabris. Petioli ca. 1 cm. longi, supra canaliculati, glabri. Laminae subcoriaceae late ellipticae usque ad 13 cm. longae 8.5 cm. latae, abrupte breviterque acuminatae, basi abrupte lateque cuneatae, juventute utrinque minutissime lepidotae maturitate fere glabrae, 5-nerviæ, venis secundariis sub angulo ca. 70° adscendentibus, 5-10 mm. distantibus. Inflorescentia paniculiformis pedunculata 5 cm. longa; pedicelli 3-6 mm. longi. Hypanthium campanulatum 3.7 mm. longum, minute furfuraceum. Calycis tubus erectus 0.8 mm. longus; lobi suberecti a sinibus acutis, late ovati, subacuti, 0.6 mm. longi. Petala triangulari-ovata alba, 2.8 mm. longa, breviter unguiculata, basi truncata, subacuta. Stamina 10 dimorpha; filamenta jam non matura; antherae breviores lineares 3.1 mm. longae, obtusae, 4-loculares, facile fissiles, connectivo basi paullo incrassato in lobos 3 rotundatos laterales; antherae longiores lineares 4.5 mm. longae, apice complanatae, 4-loculares, connectivo basi breviter producto, diviso in lobos 2 laterales teretes lineares deflexo-curvatos 1.5 mm. longos. Ovarium fere superum, 3(?)-loculare; stylus validus teres 6.5 mm. longus; stigma truncatum.

TYPE: *Cuatrecasas 17702*, collected at Quebrada de Guapecito, Dept. El Valle, alt. 0-5 m. The species can not be assigned satisfactorily to any section of *Miconia*. Four-celled anthers are known to me only in the section *Amblyarrhena* and a few species of *Cremanium*; in all of these the anthers are short and broad and open by a single pore. The pore was not definitely seen in our plant, but there are obviously two of them. Among hundreds of species of *Miconia* which I have carefully examined, petals and connective of this character have never been noted. However, the plant has in every way the general facies of a *Miconia*. If it is excluded from the genus, the problem of placing it elsewhere arises, and I know of no other genus to which it can be referred without doing violence to existing generic concepts.



**Miconia blakeaefolia** Gleason, sp. nov. (Sect. *Tamonea*). Liana magna, teste cl. Cuatrecasio. Caules juveniles obscure obtuseque quadrangulati, petioli, et inflorescentia minute brunneo-puberula. Petioli 6–10 mm. longi. Laminae coriaceae, violaceo-suffusae, ellipticae, usque ad 11 cm. longae 4.5 cm. latae, abrupte acuminatae, acumine saepe recurvo vel torto, integrae, basi rotundatae, 5-ply-nerviae, jugo exteriori submarginali, supra glabrae subnitentes, subtus ad paginam glabrae ad venas puberulae; venae secundariae 1.5 mm. distantes transversae. Panicula 8–12 cm. longa. Flores 5-meri sessiles. Hypanthium tubulosum, 3.6 mm. longum, glabrum. Calycis tubus erectus, 1 mm. longus; sepala fere semicircularia, 1 mm. longa a sinibus acutis, minutissime ciliata. Petala rubro-violacea, oblonga, 6–7 mm. longa, ca. 3 mm. lata. Stamina isomorpha. Filamenta gracilia, glabra, 3.8 mm. longa. Antherae anguste subulatae, valde arcuatae, 4.6 mm. longae, 2-loculares; connectivum simplex. Ovarium inferum, 5-loculare; stylus glaber, crassus, 5 mm. longus, summo curvatus; stigma capitatum, 0.8 mm. latum.

TYPE: *Cuatrecasas 15181*, collected at Piedra de Moler, on the western slope of the Cordillera Occidental, Dept. El Valle, alt. 900–1180 m.; *14924*, from the same locality, is identical. See discussion under *M. transversa*.

**Miconia transversa** Gleason, sp. nov. (Sect. *Tamonea*). Arbor 10 m. alta, ubique glabra. Caules subteretes. Petioli 6–12 mm. longi. Laminae coriaceae, virides, oblongo-ellipticae, usque ad 15 cm. longae 5.5 cm. latae, abrupte acuminatae, acumine 8–10 mm. longo, integrae, basi longe cuneatae, 5-ply-nerviae; venae secundariae transversae, 1.5–2 mm. distantes. Panicula ramosa, ca. 12 cm. longa. Flores sessiles, 5-meri. Hypanthium tubulosum, 3 mm. longum. Calycis tubus erectus, fere 0.5 mm. longus, truncatus, minutissime ciliatus. Petala rosea, oblonga, 5.2 mm. longa, 2 mm. lata. Stamina isomorpha. Filamenta gracilia, 3 mm. longa. Antherae anguste subulatae, valde arcuatae, ca. 5 mm. longae, 2-loculares; connectivum simplex. Ovarium inferum 3(?)-loculare; stylus glaber, crassus, 4.5 mm. longus, summo curvatus; stigma capitatum, 1 mm. latum.

TYPE: *Cuatrecasas 17459*, collected at Silva, on the Pacific coast of Dept. El Valle, alt. 5–80 m.; *17488A*, from the same place, is identical.

The only species with which this and *M. blakeaefolia* might be confused is the mysterious *M. foliosa* Triana, not seen by Cogniaux, not found by me in European herbaria, not photographed by Macbride. One clause of Triana's description, "calycis . . . limbo . . . obtuse 4?-lobo," may suggest that he had very scanty material. Our *M. blakeaefolia* differs from Triana's description in its pubescence and its leaves rounded at base; *M. transversa* differs in its truncate calyx; both differ in their slender petioles and distinctly pty-nerved leaves.

**Miconia centronioides** Gleason, sp. nov. (Sect. *Adenodesma*). Arbor magna, ramis ultimis, petiolis, pagina foliorum inferiori, inflorescentia, hypanthiis, calycibus arctissime cinereo-stellato-lepidotis. Petioli validi 2–3 cm. longi. Laminae firmas anguste obovatae, usque ad 15 cm. longae 7 cm. latae, superne rotundatae ad apiculum parvum triangularem, basi cuneatae, superne glabrae lucidae, 3-nerviae, jugo marginale neglecto. Inflorescentia terminalis brachiata ca. 2 dm. longa, ramis arcte adscendentibus. Flores numerosi breviter pedicellati 5-meri. Hypanthium hemisphaericum 3 mm. altum, supra ovarium valde incrassatum ovarium fere obtegens, toro ergo

centrali. Calyx 3 mm. longum exacte truncatum paulo ampliatus, dentibus externis 5 minutis notatum. Petala rosea obovato-oblonga 19 mm. longa 12 mm. lata, superne rotundata, extus cinereo-lepidota. Stamina fere isomorpha. Filamenta glabra 9.5 mm. longa. Antherae subulatae 6.7 mm. longae, thecis in parte inferiore valde convolutis superne rectis attenuatis ad porum ventro-terminalem. Connectivum prope basin incrassatum canaliculatum circum bases thecarum curvatum et incrassatum densiuscule glandulosum. Ovarium 5-loculare; stylus sigmoideus glaber 14 mm. longus; stigma petatum 2.3 mm. diam.

TYPE: *Cuatrecasas 14145*, collected on the Rio Micay, Dept. Cauca, alt. 5-20 m. *Cuatrecasas 17676*, from Quebrada de Guapecito, Dept. del Valle, alt. 0-5 m. is conspecific; its leaves are up to 22 by 10 cm. and the calyx is 4 mm. long. The glandular subulate anthers place it in the section *Adenodesma*; its greatly thickened hypanthium associates it with *M. arinaeoides* Gl. and *M. megalantha* Gl. The latter is especially similar to *M. centronioides*, but is distinguished by its larger leaves nearly glabrous beneath, glandular filaments and style, slightly dimorphic anthers, and ovary with flaring summit.

***Miconia platypoda*** Gleason, sp. nov. (Sect. *Eumiconia*, *Diplostachyeae*) Frutex, caulibus arcute brunneo-stellato-tomentosis atque petiolis et inflorescentiis, pilis sessilibus multiradiatis. Petioli 10-18 mm. longi valde lateraliter compressi. Laminae anguste elliptico-oblongae, usque ad 18 cm. longae 5 cm. latae, acuminatae, integrae, basi cuneatae, 3-ply-nerviae, jugo marginali obscuro neglecto, juveniles utrinque sparse stellatae, mox glabrescentes. Spicae 3, 5-10 cm. longae; flores 4-meri sessiles, solitarii vel bini. Hypanthium ellipsoideum, 2.4 mm. longum, sparse griseo-stellatum. Calycis tubus 0.4 mm. altus; sepala triangularia, a toro 1.1 mm. longa. Petala alba, obovata, 1 mm. longa, erecta. Stamina isomorpha. Filamenta gracilia, 1.2 mm. longa. Antherae anguste lineares, 1.8 mm. longae, 2-loculares. Connectivum infra thecas 0.2 mm. productum in lobos 2 laterales. Ovarium seminferum, glabrum; stylus cylindricus, 4.3 mm. longus; stigma truncatum.

TYPE: *Cuatrecasas 7185*, collected at Cerro de Circasia, Vaupés, alt. 300-500 m. We have here the first known relative of *M. marginata* Triana, which has a similar inflorescence, petals, stamens, and stigma. In it the foliage and hypanthium are glabrous, the lateral nerves of the leaf are strictly marginal, and the margin of the leaf is peculiarly reflexed.

*Miconia gracilis* Tr. No. 17338 apparently represents this species, which I have not previously noted from South America.

***Miconia stipitata*** Gleason, sp. nov. (Sect. *Eumiconia*, *Glomeratiflorae*). Frutex 2-3 m. altus, caulibus dense hirsutis, pilis stipitato-stellatis. Petioli 5-10 mm. longi, stipitato-stellati. Laminae tenues, anguste ovato-lanceolatae, acuminatae, integrae, basi cordatae, 3-nerviae, jugo marginali neglecto, utrinque stipitato-stellatae. Panicula ramosa; flores sessiles 5-meri ad apicem ramulorum. Hypanthium anguste campanulatum, 2 mm. longum, stipitato-stellatum. Calycis tubus 0.4 mm. productus; sepala depressotriangularia e sinibus acutis, a toro 1 mm. longa; dentes exteriores crasse subulati, pubescentes, sepala 0.4 mm. excedentes. Petala alba, oblonga, ca. 3 mm. longa, inaequaliter retusa. Stamina dimorpha. Filamenta gracilia. Antherae lineares, 3 vel 2.3 mm. longae, 2-loculares, poro terminali. Connectivum infra thecas 0.5 mm. productum, in ser. ext. basi truncatum, lateraliter

expansum in lobos 2 deflexos margine pauci-glandulosos, in ser. int. in lobos 2 laterales eglandulosos divisum. Ovarium semi-inferum, 3-loculare, summo glabrum; stylus rectus, teres, 4.6 mm. longus; stigma truncatum.

TYPE: *Cuatrecasas 13713*, collected at Quebrada del Cauchal, western slope of the Cordillera Occidental, Dept. El Valle, alt. 300 m. The stalk of the stellate hairs is about 1 mm. long on the stem, petioles, veins, and inflorescence, 0.5 mm. on the leaf-surface, and still shorter on the hypanthium. Pubescence of this type is relatively uncommon in *Miconia*, where it is particularly characteristic of *M. barbinervis* (Benth.) Tr., *M. stelligera* Cogn., and *M. clavistila* Gl. Our plant differs from all of these in its dimorphic glandular stamens; in the first of the three the leaves have simple bristles on the upper side and in the other two they are essentially glabrous.

MICONIA LANATA (DC.) Tr. 16969. A species of Guiana and the Amazonian lowlands, not heretofore seen by me from Colombia.

MICONIA COMPACTA Gleason (1931; *M. semota* Markg. 1934). Originally described from Iquitos, Peru, the species now appears in the Vaupés region of southeastern Colombia (6939).

MICONIA RUFICALYX Gleason. Heretofore known only from British Guiana (16745).

MICONIA PILGERIANA Ule. A fairly well known species of the lowlands of the upper Amazon valley which now appears in southwestern Colombia (16907). It was assigned by its author to section *Cremanium* and in 1931 I suggested that it belonged better with section *Glossocentrum* because of the wide terminal pore of the anthers. The anthers at full maturity extend this pore into two longitudinal clefts, a character of section *Chaenantha*, and very closely resemble those of the Andean *M. dolichorrhyncha* Naud.

**Clidemia vallicola** Gleason, sp. nov. (Sect. *Staphidium*). Frutex vel arbuscula ramosa, ramis ultimis dense stellato-tomentosis atque glanduloso-hirsutis, pilis 0.5–1.5 mm. longis. Petioli validi 1–2 cm. longi, stellato-tomentosi et densissime hirsuti. Laminae tenues, late ovatae, usque 18 cm. longae 14 cm. latae, abrupte acuminatae, fere integrae, basi cordatae, 5–7-nerviae, supra minute glandulosae, pilis 0.2 mm. longis, subtus ad paginam sparse glandulosae, pilis 0.1 mm. longis, ad venas glanduloso-setosae. Inflorescentiae axillares paniculiformes, ramis paucis ultra medium paucifloris. Flores 7-meri. Hypanthium campanulatum supra ovarium constrictum 4 mm. longum, dense glanduloso-hirsutum. Calycis hirsuti tubus 1 mm. longus, lobi ovati a toro 2.3 mm. longi; dentes exteriores adnati, sepala 1 mm. excedentes, dense hirsuti. Petala obovato-oblonga 7 mm. longa. Stamina numerosa (22 enumerata) isomorpha; filamenta gracilia 4 mm. longa; antherae subulatae 2.7 mm. longae, poro dorso-terminali dehiscentes; connectivum infra thecas breviter productum et incrassatum. Ovarium 7-loculare inferum, apice minutissime glanduloso-setulosum; stylus 7 mm. longus; stigma truncatum.

TYPE: *Cuatrecasas 13735*, collected at Quebrada del Danubio, Dept. El Valle, alt. 300–350 m.; *Cuatrecasas 14401* is the same; also on the coast of El Valle, *Cuatrecasas 13998*. The nature of the inflorescence, the structure of the stamens, and the character of the pubescence show its close relationship to *C. novemnervia* (DC.) Triana. Our plant differs in its 7-merous flowers, its numerous stamens, and the pubescence of the leaves.

**Clidemia crenulata** Gleason, sp. nov. (Sect. *Sagraea*). Frutex 2 m. altus, ramis teretibus dense breviterque hirsutis, pilis glandulosis ca. 2 mm. longis. Formicaria hirsuta, persistentia ad basim petioli. Petioli hirsuti usque ad 5 cm. longi. Laminae tenues ovato-oblongae usque ad 25 cm. longae 14 cm. latae, breviter caudato-acuminatae, insigniter crenulatae, basi rotundatae paullo emarginatae, 5-nerviae, jugo submarginali neglecto, utrinque sparse hirsutae. Inflorescentiae axillares multiflorae congestae. Flores sessiles 4-meri. Hypanthium tubuloso-urceolatum 4.7 mm. longum infra medium sparse glanduloso-hirsutum. Calycis tubus 0.2–0.3 mm. productus erectus; lobi depressi late rotundati; dentes exteriores subapicales patuli 0.6–0.9 mm. longi. Petala oblonga obtusa 3.7 mm. longa. Stamina isomorpha; filamenta 3.7–4 mm. longa; antherae subulatae 4.7 mm. longae, poro apicali dehiscentes; connectivum simplex. Ovarium 4-loculare inferum; stylus gracilis glaber 11 mm. longus; stigma capitatum.

TYPE: *Cuatrecasas 16534*, collected at La Trojita, Dept. El Valle, alt. 5–50 m. It is obviously related to *C. petiolata* (Rich.) DC., differing in the pubescence of the petiole and lower leaf-surface as well as in the presence of formicaria which are persistent after the leaves have fallen.

**CLIDEMIA RAMIFLORA** Gleason var. **colombiana** (Gleason, var. nov. Frutex 1–2 m. altus, caulibus juvenilibus cum petiolis 4–6 cm. longis dense stellato-furfuraceis fere velutinis. Cymae infra folia orientes, pluriflorae trichotomae ramosae 2–4 cm. longae. Flores 4-meri. Sepala, petala, et stamina deficientes. Laminae ovatae, usque ad 23 cm. longae 15 cm. latae, abrupte acuminatae in apicem obtusum, minute serrulatae, basi late rotundatae et cordulatae, 7-nerviae, utrinque glabra praeter venas majores stellato-furfuraceas.

TYPE: *Cuatrecasas 17298*, collected at San Isidro, Dept. del Valle, alt. 5–100 m. Its assignment to *C. ramiflora* is based solely on superficial resemblance. The type differs in a closer and finer pubescence and in leaves elliptic rather than ovate.

**Clidemia panamensis** (Blake & Standley) Gleason, comb. nov. *Prosa-nerpis panamensis* Blake & Standley, Field Mus. Publ. Bot. 4: 245. 1929; *C. epiphytica*, in part, Gleason, Brittonia 3: 131. 1939. I combined the two species under the earlier name because of close similarity in foliage and calyx. More material shows that the two are distinct, the hypanthium of *C. epiphyta* being nearly glabrous, while that of *C. panamensis* is distinctly hirsute.

**Ossaea resinosa** Gleason, sp. nov. Liana epiphytica lignosa, ramis gracilibus valde elongatis, minutissime brunneo-furfuraceis. Petioli 10–15 mm. longi. Laminae tenues opacae lanceolatae, usque ad 8 cm. longae 3 cm. latae, longe caudato-acuminatae, basi rotundatae, 3-nerviae jugo submarginali neglecto, ubique praesertim subtus resinoso-punctatae. Pedunculi axillares gracillimi, usque ad 4 cm. longi, saepissime 3-flori, bracteis 2 linearibus ca. 1 cm. longis, floribus 2 axillaribus subsessilibus, 1 terminali pedicellato. Flores 4-meri. Hypanthium cum calyce ellipsoideum 3.7 mm. longum, minutissime furfuraceum. Sepala conniventia (an semper?) minuta, dentibus exterioribus crasse subulatis 0.5 mm. longis. Petala jam immatura late triangularia acuta 1.5 mm. longa. Filamenta immatura; antherae lineares vel lanceolatae 2 mm. longae, poro ventro-terminali dehiscentes; connectivum infra thecas

angustatum 0.4 mm. productum in calcar conicum. Ovarium 3-loculare; stylus gracilis jam 1.4 mm. longus; stigma punctiforme.

TYPE: *Cuatrecasas 16619*, collected at La Trojita, Dept. del Valle, alt. 5-50 m. The immature condition of the flowers does not permit as full a description as desired, but its habit, inflorescence, and resinous indument are at variance with all other described species.

THE NEW YORK BOTANICAL GARDEN  
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## JUNIPERUS VIRGINIANA, J. HORIZONTALIS, AND J. SCOPULORUM—V. TAXONOMIC TREATMENT

NORMAN C. FASSETT

These studies have been based on part or all the material in several herbaria: the Arnold Arboretum, the Gray Herbarium, the New York Botanical Garden, the University of Wisconsin, the University of Minnesota, Iowa State College, and North Dakota State Agricultural College. Herbarium material has been supplemented by mass collections from localities representing nearly the whole range of *J. virginiana*, much of the eastern part of the range of *J. scopulorum*, and a number of localities of *J. horizontalis*. The mass collections have consisted of a sample from each individual tree or shrub in a colony; by their use it has been possible to study not only individuals but populations, and to see how certain characters vary within certain small areas. Much of the collecting was made possible by grants from the Wisconsin Alumni Research Foundation.

With certain exceptions in the areas shown on Map 2, individuals of this group may be identified by the following key:

- a. Leaves<sup>1</sup> overlapping, their epidermal cells 5–20  $\mu$  wide, averaging 9–12  $\mu$ , mostly 10  $\mu$ ; not more than 33% of peduncles of female cones curved; cones maturing in one year, 2.0–6.5 mm., mostly 3.5–5.5 mm., long; nearly all seeds with shallow pits.
  - b. Trunks erect.
    - c. Height of crown 1–2 times its width. *J. virginiana*.
    - c. Height of crown 2.5–7.5 times its width. *J. virginiana* var. *crebra*.
  - b. Matted shrubs, with stems creeping or somewhat ascending. *J. virginiana* var. *ambigens*.
- a. Leaves overlapping or not, their epidermal cells 5–35  $\mu$  wide, averaging 13–19  $\mu$ , mostly 15  $\mu$ ; 8–100% of peduncles of female cones curved; cones mostly maturing in two years, 4–9 mm., mostly 5.5–6.5 mm., long, seeds pitted or not.
  - d. Leaves rarely overlapping and then but slightly, their tips blunt; foliar glands longer than the distance from the gland to the tip of the leaf; 8–70% of peduncles of female cones curved; seeds nearly all with deep pits about half the length of the seed; trees, or shrubs with ascending branches about 1 m. high.
    - e. Trees with erect or strongly ascending trunks.
      - f. Height of tree 1–2 times its width. *J. scopulorum*.
      - f. Height 2.5–3.0 times width. *J. scopulorum* var. *columnaris*.
    - e. Depressed shrubs. *J. scopulorum* var. *patens*.

<sup>1</sup> In each case the mature scale-like leaves are meant. Acicular leaves have the width of epidermal cells characteristic of the species, but do not show the differences in overlapping or in leaf tips. All the specific characters have been discussed in detail in paper I of this series, Bull. Torrey Club 71: 410–418.

*d.* Leaves mostly overlapping, their tips apiculate; foliar glands shorter than the distance from the gland to the tip of the leaf; 80–100% of peduncles of female cones curved; about half the seeds with shallow pits less than half the length of the seed; prostrate matted shrubs.

*J. horizontalis.*

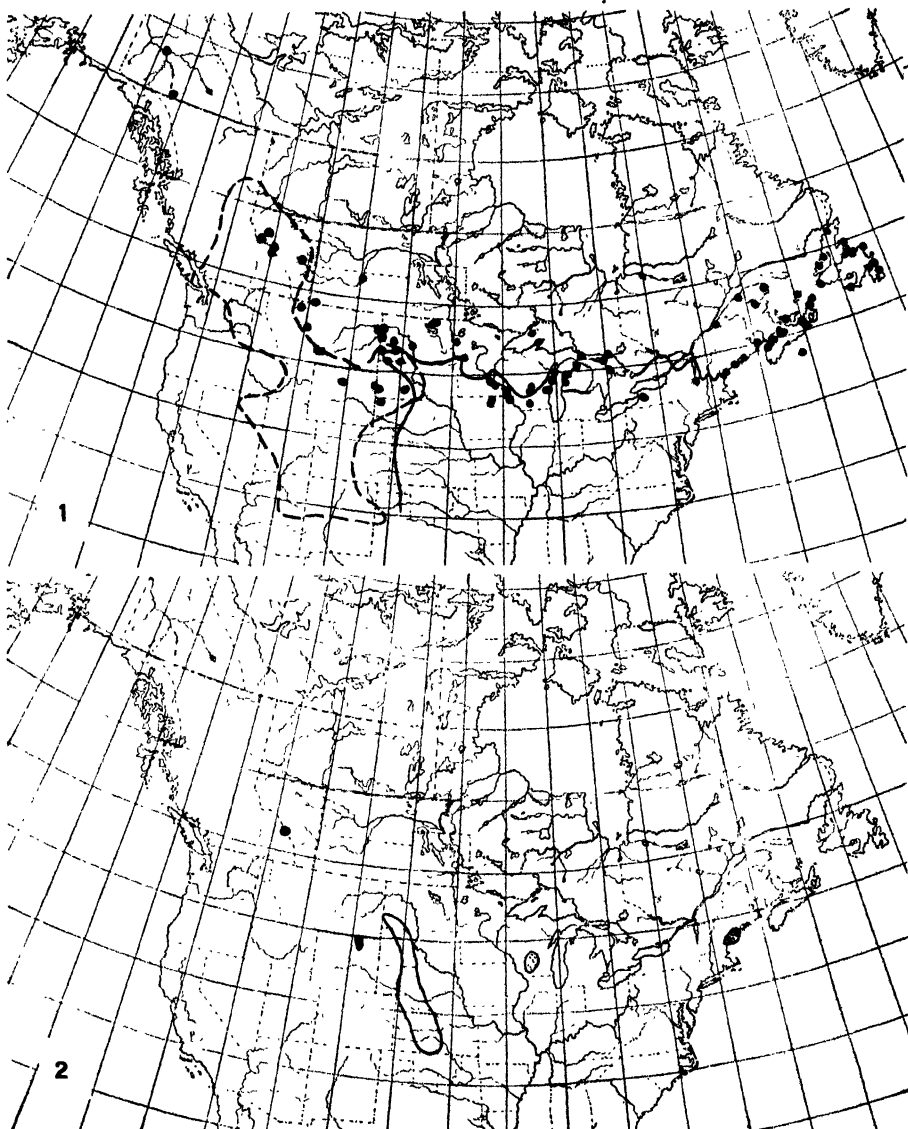


FIG. 1. Heavy solid line: approximately northern and western limits of *J. virginiana*. Heavy broken line: approximate limits of *J. scopulorum*. Dots: range of *J. horizontalis*. FIG. 2. Stippled areas: regions of probable crossing of *J. virginiana* and *J. horizontalis*—*J. virginiana* var. *ambigua*. Area enclosed by heavy line: region of hybrid swarms of *J. virginiana* and *J. scopulorum*. Solid black areas: localities for *J. scopulorum* var. *patens*.

1. *J. VIRGINIANA* L. Sp. Pl. 1039. 1753. Southern Maine, southern Ontario, southern Wisconsin and southwestern North Dakota, southward (fig. 1, heavy solid line). The southern limits are not determined, since the relation of this species to *J. silicicola* (Small) Bailey and *J. lucayana* Britton has not been studied.

1a. *J. VIRGINIANA* var. *CREBRA* Fernald & Griscom, *Rhodora* **37**: 133. 1935; description and range amended by Fassett, *Am. Jour. Bot.* **30**: 469-477. 1943. Locally replacing the typical form of the species in New England, eastern and central New York, New Jersey to western Virginia; northern Indiana to southeastern Wisconsin; southern Indiana; Knoxville, Tennessee; southern Missouri.

1b. *J. VIRGINIANA* var. *AMBIGENS* Fassett, *Bull. Torrey Club* **72**: 380. 1945. In areas of overlap of the range of *J. virginiana* with *J. horizontalis*, and probably the result of hybridization between these two species, on the coast of Maine from Lincoln County to York County. Although most individuals may be identified as this variety or as one of the purported parent species, some plants may show various other combinations of characters.<sup>2</sup>

2. *J. SCOPULORUM* Sargent, *Gard. & For.* **10**: 420. 1897. South Dakota to eastern Nevada and Vancouver Island, north into British Columbia and Alberta, south to northeastern Arizona and northwestern Texas (heavy broken line, fig. 1). Where the range overlaps or approaches that of *J. virginiana* (region enclosed by a heavy black line on figure 2), the characters of the two species occur in many recombinations,<sup>3</sup> and many individuals cannot be identified by the key.

2a. *J. SCOPULORUM* var. *columnaris* Fassett, var. nov. Arbor altitudine latitudinem 2.5-3.0-pie. NORTH DAKOTA: bottom of deep gully, edge of pine region, Amidon, Slope County, May 15, 1941, *O. A. Stevens* 504 (TYPE in Herb. North Dakota Agricultural College). Dr. Eltar Nielsen sends me a photograph of a similar tree at Spanish Point, near Williston, North Dakota.

2b. *J. SCOPULORUM* var. *PATENS* Fassett, *Bull. Torrey Club* **72**: 46. 1945. On the west slopes of the Big Horn Mountains, Wyoming, and about Banff, Alberta; doubtless elsewhere (solid black areas, fig. 2). Perhaps a hybrid with *J. horizontalis*.<sup>4</sup>

3. *J. HORIZONTALIS* Moench, *Meth.* 699. 1794. Locally from Newfoundland and southern Maine, westward along the Great Lakes; Wisconsin, Iowa and Minnesota to northwestern Nebraska and northern North Dakota to Montana; northwestward to Yukon Territory (dots, fig. 1).

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<sup>2</sup> See paper IV of this series, *Bull. Torrey Club* **72**: 379-384.

<sup>3</sup> See paper II of this series, *Bull. Torrey Club* **71**: 475-483.

<sup>4</sup> See paper III of this series, *Bull. Torrey Club* **72**: 42-46.



# INDEX TO AMERICAN BOTANICAL LITERATURE

## PLANT TAXONOMY AND FLOBISTICS

(exclusive of fungi)

(See also under Genetics, Goodwin)

- Aberg, E. & Weibe, G. A.** Irregular barley, *Hordeum irregulare*, sp. nov. Jour. Wash. Acad. 35: 161-164. f. 1. 15 My 1945.
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(including anatomy, and cytology in part)

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(See also under Genetics; **Hollaender**)

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(including cyto-genetics)

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## THE SHOOT OF BOTRYCHIUM INTERPRETED AS A SERIES OF DICHOTOMIES

M. A. CHRYSLER<sup>1</sup>

It has long been recognized that Ophioglossales exhibit a number of primitive features, especially in their sporangia, while they possess certain unusual features which distinguish them from Filicales, with which group there has been a persistent tendency to associate them. This was but natural on account of the fern-like sterile segment of the leaf in *Botrychium*. But the discovery of the Coenopteridales followed by that of Psilophytales has led to attempts to reinterpret the morphological features of Ophioglossales. This is notably true of Zimmermann's attempt to fit *Botrychium Lunaria* into his "Telomtheorie"; especially interesting is his hypothesis (1930, p. 203) that the fertile spike represents one branch of an ancient dichotomy in the plane perpendicular to that of the other divisions occurring in the leaf. Such a conjecture, if supported, would indicate a relation of the order to certain Coenopteridales and Rhyniaceae. This interpretation of the fertile spike was promptly taken up by Bower (1935), replacing the theories which he earlier entertained. Zimmermann's definition (1930, p. 65) of a telome (fertile or sterile) as an ultimate branch of a shoot, including its vascular bundle, constituting the morphological unit of the cormophyte shoot, was supplemented in 1938 by addition of the term *mesome* to express the idea of two or more telomes fused as they appear below a dichotomy. The two terms will in this paper be employed as thus defined. No attempt is here made to define a dichotomy in terms of development; the recent review by Sifton (1944) of the literature on the question as to what constitutes a dichotomy shows a notable lack of agreement among the workers in this field.

Since the presence of a vascular bundle characterizes a telome, the behavior of the bundles of the shoot in Ophioglossales should afford critical evidence as to the soundness of Zimmermann's interpretation of the fertile spike. He makes only slight reference to evidence from anatomy; it is the purpose of this study to investigate the evidence from this point of view. The genus *Botrychium*, generally regarded as the most primitive of the genera, has been found to be the most favorable for the purpose. The following species, named according to Clausen's memoir (1938), have been available:

Subgenus *Eubotrychium*.

*B. boreale* Milde: Sweden (herbarium material).

- *B. lanceolatum* (Gmel.). Angstr., subsp. *angustisegmentum* (Pease & Moore) Clausen: Me., N. J., N. Y., Pa.

<sup>1</sup> Publication of the Bureau of Biological Research, Rutgers University.

*B. Lunaria* (L.) Sw., var. *typicum*: Gaspé, Europe.

*B. Lunaria*, var. *minganense* (Victorin) Dole: Que. (herbarium material).

*B. matricariaefolium* A. Br., subsp. *typicum*: Me., N. J., N. Y., Pa., Gaspé.

*B. pumicola* Coville: Ore.

*B. simplex* Hitchc., var. *compositum* (Lasch) Milde: Cal.

*B. simplex* Hitchc., var. *tenebrosum* (A. A. Eaton) Clausen: Me., N. J., N. Y.

Subgenus *Sceptridium*.

*B. dissectum* Spreng. and var. *obliquum* (Muhl.) Clute: Me., N. H., N. J., Pa.

*B. multifidum* (Gmel.) Rupr., ssp. *typicum*: Pa., Gaspé.

*B. multifidum*, ssp. *silaifolium* (Presl) Clausen: N. H.

*B. underwoodianum* Maxon: Costa Rica (herbarium material).

Subgenus *Osmundopteris*.

*B. lanuginosum* (Wall.) Hk. & Grev.: Sumatra (herbarium material).

*B. virginianum* (L.) Sw.: N. J., Gaspé.

The object of securing material from widely separated localities was to be sure that climatic differences were not the cause of variations in anatomical structure. Plants differing considerably in size have been included. Material of *B. dissectum* and *multifidum* showing abnormalities such as extra fertile branches have also been examined. I am greatly indebted to the following sources of material: Professor R. T. Clausen, Mr. W. L. Dix, Mr. J. L. Edwards, Mr. G. G. Nearing, Brooklyn Botanic Garden, Gray Herbarium, Herbarium of University of California at Berkeley. In all cases the material was imbedded in paraffin and serial sections cut through the branching regions. One fortunate fact about members of this order is that the bud located at the base of the petiole of the present year's leaf contains an epitome of the leaf architecture, and requires the preparation of much fewer sections, although it has the disadvantage that the vascular tissues are still in a more or less immature stage.

#### OBSERVATIONS

What appears to be the primitive condition of the vascular system is best seen in members of the subgenus *Eubotrychium* (Milde) Clausen. All species of this group have been studied, and have been found to show a remarkable uniformity in their vascular plan; in fact individuals of one species may vary almost as much as do different species. *B. matricariaefolium* will first be considered. From the hollow central cylinder of the vertical rhizome arise a series of leaf traces which do not seem to show a definite phyllotaxy (see figure 25 representing *B. dissectum*); in some plants the distichous arrangement is approached. The bundle leaves the stele as a somewhat curved group of tracheids most of which are arranged in radial rows, as are the tracheids found in the stele; before the bundle reaches the region of the petiole, however, this "carry-over" of secondary structure disappears and the trace assumes the form of a collateral endarch bundle with a single protoxylem group (figs. 1, 5) which soon divides and at once the bundle splits into a right and a left half, each with a single protoxylem (figs. 2, 6). This doubling

of the trace usually occurs at the level where it emerges from the rhizome into the petiole, but may occur as much as 2 mm. above this level. In a strongly growing leaf the size of the trace may approach that of the remaining part of the stele (fig. 12), suggesting a dichotomous division of the vascular system. As the two petiolar strands rise each gradually rotates through nearly  $90^\circ$  so that their xylems face one another (fig. 3). Each bundle meanwhile increases considerably in size and assumes a curved form like a parenthesis (fig. 4), the protoxylem of each divides, and just below the level where fertile and sterile branches of the leaf separate, each bundle divides in the radial plane into two more or less equal parts (fig. 7), the size of each depending on the relative size of the two leaf-branches. This division is of course at right angles to the preceding division. Two bundles, one from each "parenthesis," diverge to the sterile branch, where they again undergo a rotation which brings their edges side by side and their xylems facing the fertile segment, i.e., adaxial (fig. 8); each bundle again divides into a right and a left portion, more or less unequally, and these divisions may occur at the same level or one ahead of the other; by a repetition of this process the vascular skeleton of the sterile branch is built up. Returning to the parenthesis, the two bundles which did not diverge run up into the sporogenous region of the fertile branch; they do not rotate through as great an angle as occurs in the sterile branch (figs. 8, 28), but at a higher level undergo fission, the lateral bundles supplying branches which eventually lead to sporangia, each with its bundle (fig. 28). It should be noted that the members of a pair of parentheses do not always divide at the same level, (fig. 9)—each behaves independently in this regard.

With respect to the other species in subgenus *Eubotrychium*, *B. Lunaria* can hardly if at all be distinguished from *B. matricariaefolium* by the vascular tissues. The same can be said of *B. boreale* and of *B. Lunaria* var. *minganense*. In *B. lanceolatum* the same general plan is present, but the parentheses undergo partial segregations (fig. 11) before the ab- and adaxial portions break off to supply the sterile and fertile branches respectively. The reason for this appears at once upon inspection of a plant; in this species the sterile and fertile branches typically divide very quickly after their separation; this feature is represented in the vascular structure by a precocious separation of the strands which lead to the various pinnae, etc. That is, there is an overlapping or telescoping of the dichotomies which were traced in the preceding paragraph. The result is that a pair of parentheses expands into what simulates a dictyostele; the units supplying the sterile branch, however, soon diverge and assume the form of a flattened row such as is characteristic of the plainly dorsiventral blade. *B. simplex*, especially the variety *tenebrosus*, in keeping with the slender form has smaller, more rounded bundles than occur in the larger species, but exactly the same series of

dichotomies of the petiolar trace are found. In *B. simplex* var. *compositum* the form and course of the bundles seem exactly the same as in *B. matricariaefolium*. The rare species *B. pumicola* (material from Dr. Clausen) presents one additional feature of interest. In the form and course of the bundles this species is similar to *B. simplex*, except that the two bundles belonging to the sterile branch divide before separation of the sterile from the fertile branch, i.e., lower than in the stage shown in figure 8. Hence six bundles (three pairs) traverse the common stalk for a distance of several millimeters. This condition is readily explained by the short stalk of the sterile branch (cf. *B. lanceolatum*).

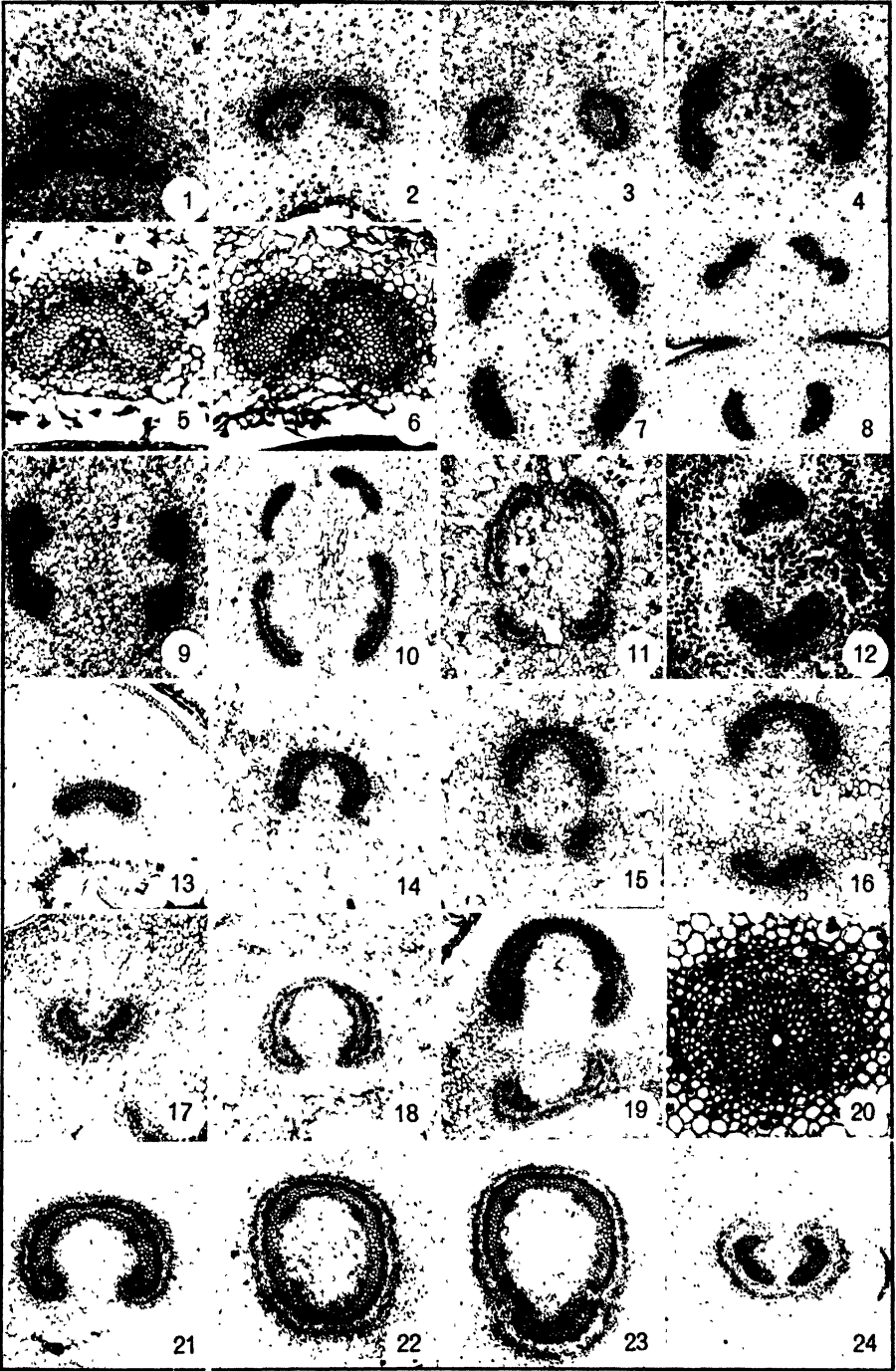
In the subgenus *Sceptridium* Clausen (the group *Ternata* of Prantl) a different appearance is presented, and this is exhibited in all the species which have been available for study. *B. multifidum* is chosen to illustrate what may be regarded as the typical condition. The leaf-trace presents the same structure as in *Eubotrychium*, namely, it arises from the solenostele of the rhizome as a slightly curved bundle, at first with secondary xylem; later it is seen to possess a single protoxylem which at a slightly higher level divides (fig. 13). Unlike *B. matricariaefolium*, however, the trace remains undivided (except in rare cases, *vide infra*). As it rises through the petiole it becomes more curved and takes the form of a C (fig. 14), the edges of which close in toward one another so that a rather narrow opening remains. Meanwhile each of the two protoxylems divides, and from each edge of the C a rather small bundle separates (fig. 15), carrying a single protoxylem. These two bundles rotate so that their xylem groups come to face the C; they constitute the vascular supply of the fertile branch or spike (Chrysler 1910, p. 6). These bundles generally approach one another and for a short distance in their course are fused (fig. 16) edge to edge, but at a higher level separate (fig. 17). (The further branching in fertile and sterile segments will be

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#### Explanation of figures 1-24

In all the figures the stem axis is toward the bottom of the page.

FIGS. 1-8. *Botrychium matricariaefolium*: 1-4, 7, 8, from a series through petiole; figure 4 shows the "parenthesis" stage; figures 5, 6 from another series show the protoxylem groups. Figs. 1-4, 7,  $\times 18$ . Figs. 5, 6,  $\times 37$ . Fig. 8,  $\times 14$ . FIG. 9. *B. Lunaria*: similar to figure 7, but one parenthesis divided before the other.  $\times 22$ . FIG. 10. *B. matricariaefolium*: same stage as figure 7, bundles leading to fertile branch are larger than the others.  $\times 12$ . FIG. 11. *B. lanceolatum* var. *angustisegmentum*: slightly earlier stage than figures 7, 10; the bundles form a pseudostele.  $\times 24$ . FIG. 12. *B. multifidum*: leaf-trace (above) comparable in size with the stele.  $\times 24$ . FIGS. 13-17. *B. multifidum*, illustrating Plan 1, from series corresponding to figures 1-8. Note absence of stage corresponding to figure 2. Figure 17, through the fertile branch, shows that the fusion in figure 16 is temporary.  $\times 22$ . FIGS. 18, 19. *B. multifidum*, illustrating Plan 3. Here the division corresponding to figure 2 does occur.  $\times 14$ . FIG. 20. *B. multifidum*: form of bundle found in fertile branch of certain small individuals.  $\times 86$ . FIGS. 21-24. *B. dissectum*, illustrating Plan 2. In figure 22 the edges of the petiolar bundle (fig. 21) have fused producing a pseudostele. Figure 24 illustrates the ultimate splitting of the bundle in the fertile branch.  $\times 17$ .



described later.) The foregoing method of branching, which we may call Plan 1, has been traced in 25 series of *B. multifidum* and varieties and *B. dissectum* and varieties. In three series is seen another mode which will be called Plan 2: the petiolar trace, at first only slightly curved, becomes more and more C-shaped and the gap in the C closes (figs. 21, 22) so that what might be called a solenostele results; this breaks into two unequal pieces lying in the radial plane (fig. 23). The smaller portion runs up into the fertile branch, and may (1) divide into two bundles lying side by side (fig. 24), or (2) become more curved so that it eventually becomes concentric (fig. 20); the latter condition has been observed only in a small plant of *B. multifidum* var. *typicum* collected on an exposed hillside pasture in the Gaspé. In three series still another mode (Plan 3) occurs; the petiolar trace begins as usual as a slightly curved bundle; at about the level of the closing of the basal sheath the trace divides (fig. 18) into a right and left half (in one case the xylem divides but the phloem remains undivided). The bundles rotate so as to face one another; meanwhile they grow and appear like a pair of parentheses from the adaxial ends of which break off the small bundles supplying the fertile segment (fig. 19). This plan is manifestly very similar to the typical behavior of members of *Eubotrychium* and is an interesting link between the two groups.

A partial series through a dried specimen of *B. underwoodianum*, collected in the mountain region of Costa Rica, has been prepared. Toward the base of the petiole the bundle is C-shaped, becoming more triangular as it ascends; the margins curl inward and fuse, producing a deltoid pseudostele; this assumes a more elliptical form and splits into two nearly equal parts, ab- and adaxial, the latter supplying the fertile branch. Whether or not this specimen is typical of the species, its vascular system illustrates Plan 2.

In subgenus *Osmundopteris* (Milde) Clausen, the only representative which has been carefully studied is the common *B. virginianum*. The course of the vascular bundles of the leaf of this species was described in 1910 by the writer, and has been reexamined in the course of the present study. As in the other species, the petiolar trace is at first a curved bundle which becomes definitely C-shaped. At about the level of the top of the basal sheath it splits into a right and a left half (cf. *Eubotrychium*). In many plants a small strand is cut off from the abaxial edge of each of the two petiolar bundles, and strong plants may show further divisions before the region of branching is reached. A short distance below the level at which branching is externally visible, a pair of almost circular bundles break off in the extra-marginal manner to supply the fertile branch (Chrysler 1910, p. 2, 3). A short distance further up in the sterile branch two strands, which may be paired, break off in the same manner to supply the two lowest divisions of the more or less ternate sterile branch. The process is repeated further up in both sterile and fertile branches.

The branching regions from two plants of *B. lanuginosum* (herbarium material) have been made into series. From these it can be made out that the vascular supply of the fertile branch arises extra-marginally as a pair of bundles which face each other and become more or less divided. Branches of the sterile segment also arise extra-marginally.

#### DISCUSSION

An attempt will now be made to interpret the foregoing observations in terms of Zimmermann's theory of telomes. This is the proposition: the shoot of *Botrychium* consists of a congeries of branches—telomes or mesomes—arising by the process of repeated dichotomy. The first dichotomy separates the leaf from the rhizome (dichotomy I). This is less apparent than the subsequent dichotomies on account of difference in external form of the two resulting mesomes (especially dorsiventrality of at least part of the leaf), also in size and shape of the two branches of the vascular system, viz., solenostele and leaf trace. Probably many of us have entertained the idea of morphological equivalence of the vascular axes in leaf and stem in a fern (e.g., Tansley 1908, p. 130), but Zimmermann definitely enunciates the idea in his paper on the stem (1930a, p. 46 and fig. 5). The difference between stele and leaf trace is largely a relative matter, as may be illustrated by the photograph of a transverse section through the rhizome of *Adiantum pedatum* bearing a large leaf (fig. 26); the uppermost branch of the vascular system is a leaf trace because the series shows that it assumes a C-shape while the lower branch closes the gap and resumes the form of a solenostele. Attention has already been called to an example (fig. 12) in which the size of a leaf trace of *Botrychium* approaches that of the stele. The axial system of *Botrychium* may thus be interpreted as a sympodium, the planes of division being radial, but not in a single plane as are the distal divisions of the sterile branch (fig. 25).

The splitting of the petiolar trace, usually at a slightly higher level than the separation of leaf-base from stem, found in all species of *Eubotrychium*, is here regarded as indicating a second dichotomy (II), although not involving division of the petiole into two mesomes. It should be recalled that distal to this division the vascular system of the leaf in say *B. Lunaria* consists of two parts, right and left, which are independent of each other except at the extreme tip, where fusions occur. Moreover the position assumed by the pair of bundles, namely, facing each other (fig. 4), is what would be expected in case a second dichotomy took place in a plane at right angles to that of dichotomy I. In some species of *Ophioglossum* a single trace may split into an indefinite number of bundles in the common stalk, while in other species the trace may be double from the very outset, i.e., its exit from the stele. The latter condition occurs in *O. Engelmanni* and is illustrated in figure 32; the

double leaf trace is to be seen also in sections of *O. fibrosum* kindly furnished by Professor Maheshwari of Agra, India, and mentioned in his account of this species (1934). It is quite possible that such early splitting of the leaf trace represents a (downward) phylogenetic slide of dichotomy II; the striking differences in level of dichotomy III, culminating in the pronounced upward slide exhibited by *B. lanuginosum* (Chrysler inedit.) may be adduced as evidence supporting this view. The frequency of a pair of bundles in the stipe of Polypodiaceae is not always realized; Waters (1928) found this condition in twelve genera of ferns of the Northeastern States, the chief exceptions occurring in such highly organized genera as *Polypodium*, *Poly-stichum* and *Dryopteris*. That the double trace goes far back in the history of fern-like plants is indicated by its occurrence in a number of Paleozoic plants, the classic example being *Lyginopteris* in which Potonié showed that the rachis itself forked (quoted by Scott, 1923, part II, p. 42). It has earlier been argued that the double vascular supply of the fertile branch in *Botrychium* indicates the dual nature of the branch, and forking examples (Chrysler 1910, fig. 28) have been adduced as supporting evidence.

Returning to *B. matricariaefolium*, the third division of the bundles takes place in the radial plane, perpendicular to that of dichotomy II, and is accompanied by the forking of the common axis, resulting in the separation of the fertile and sterile branches; this constitutes dichotomy III. Division of the bundle ("parenthesis") on one side may lag behind that of the other (fig. 9), as might be expected when two axes are concerned. The subsequent dichotomies of sterile and fertile branches are in a plane approximately at right angles to that of dichotomy III (fig. 28). It appears then that in *Eubotrychium* the entire shoot may be interpreted in terms of telomes, the dichotomies alternating in two planes for four divisions after which dorsiventrality is established. Lack of separation of telomes is covered by Zimmermann's term mesome, and is apparently represented by dichotomy II and in many divisions of the distal regions.

In *Sceptridium* the appearance of a single U-shaped bundle in the common stalk, instead of the pair of bundles characteristic of *Eubotrychium*, may be regarded as the result of disappearance of dichotomy II from the ontogenetic series. According to the alternate view, the U-shaped trace would be regarded as primitive and the dual trace as derived. That the first of these alternatives is the more probable is indicated by the following considerations: (1) splitting of the petiolar bundle (dichotomy II) has been found in several individuals (Plan 3) which otherwise belong in *Sceptridium*; (2) there is frequently a marked narrowing of the xylem at the median region of the bundle; (3) two protoxylem groups are present in the bundle of the common stalk; (4) alternation in direction of the divisions to be expected until dorsiventral structure becomes established; (5) in this subgenus



fusions of the bundles are common at various levels, the most marked and constant case being the temporary fusion immediately after dichotomy III (fig. 16); (6) the condition ultimately reached (e.g., in distal regions of the fertile branch; fig. 17), is essentially the same as in *Eubotrychium*, that is, the leaf has a right and a left half; (7) division often takes place on one side of the U before it occurs on the other side, indicating independence in behavior of the two sides of the U, corresponding to what frequently occurs in the division of the parentheses of *Eubotrychium*.

If on the other hand the condition found in *Sceptridium* is regarded as primitive rather than derived, Plan 2 would probably represent the earliest condition, with the separation of the leaf trace from the stele representing a dichotomy in a radial plane, following by the "repairing" of a solenostele in petiole as well as rhizome, and a subsequent dichotomy of the petiolar solenostele into two C-shaped parts, each of which later undergoes another dichotomy, this time in the plane at right angles to the earlier ones. If this alternative be adopted, Plan 3 would involve the interpolation of a dichotomy of the petiolar trace at about the level at which the petiole breaks off; hence *Eubotrychium* would represent an offshoot from *Sceptridium*. Derivation of Plan 1 from Plan 2 is not so obvious, but it may be remarked that in some of the plants classified as Plan 1 the C-shaped petiolar strand *almost* closes just before the two bundles break off to supply the fertile branch; such cases form a link between Plans 1 and 2—the question is, in which direction are we to read the sequence? If it insisted that the undivided C-shaped trace of *Sceptridium* (vs. the double trace of *Eubotrychium*) represents the primitive condition of the genus, the interpretation of the later branchings of the vascular system in terms of a series of dichotomies becomes strained, and surely we would be safer in regarding the fertile spike as the equivalent of two basal branches (pinnae) of the leaf.

From the standpoints of (1) geographic distribution, (2) the much divided leaves, and (3) type of development of the sporophyte generation, Clausen (1938, p. 22) has argued that *Sceptridium* is the most primitive division of the genus, although he admits that the reflexed type of vernation may be a derived condition. The difficulty in making decisions on such points is illustrated by the fact that the gametophyte of *Ophioglossum* appears to be more primitive than that of *Botrychium*, although the sporophyte of *Ophioglossum* is relatively advanced. Again, it is possible that *Eubotrychium* represents a tendency to reduction in size (consider *B. simplex* var. *tenebrosum*). When writing in 1910 I was much impressed by evidence in favor of this view (*v. infra*, on the extra-marginal origin of leaf traces). But this was several years prior to the appearance of the epoch-making papers on *Rhynia* by Kidston and Lang (1917–21).

In *Osmundopteris* dichotomy I is followed by dichotomy II, as in *Eubo-*

*trychium*. It is less certain that the cutting off of the small distal strands constitutes another dichotomy, and the extra-marginal method of origin of the strands leading to the fertile branch complicates—although it does not contradict—the interpretation of the origin of the fertile spike as the result of an antero-posterior dichotomy (III).

**Marginal and Extra-Marginal Origin of Branch Bundles ("Pinna Traces").** In *Eubotrychium* branching of vascular bundles uniformly takes place as an obvious dichotomy (figs. 8, 28); the bundle is divided, equally or unequally, into two parts by a splitting which passes through xylem and phloem. This mode of division, when occurring in a pinna trace, is called *marginal* by Bower (1923, vol. 1, p. 172). In both sterile and fertile parts of *Sceptridium* and *Osmundopteris*, however, a branch bundle frequently arises not from the edge but from the side of the C (fig. 27), leaving a temporary gap in the C. This mode of origin of a branch trace is called *extra-marginal* by Bower, who speaks of it as characteristic of large leaves. Bower moreover regards the latter method as derivative; this naturally follows if the fern leaf is held to be a sympodium, the evidence for which seems to be overwhelming. The present study has furnished support for the view that the extra-marginal method is characteristic of large leaves, e.g., its occurrence only in *Sceptridium* and *Osmundopteris*. Further, in the latter subgenus this method is found in connection with the origin of the larger (basal) branches in both fertile and sterile segments, while only the marginal method is apt to occur in smaller (distal) branches (cf. Bower's observations on *Trismeria* (1923, p. 173). It is notable that in *Sceptridium* the pair of bundles which supply the fertile spike typically arise strictly from the margin of the much curved C; in only one series, prepared from a plant of *B. dissectum* chosen on account of its having the common stalk 6 mm. in diameter, has even a slight approach to the extra-marginal method been observed at the forking region (figs. 29–31). *Osmundopteris* contains the largest plants of the genus, and it has already been recorded that in *B. virginianum* and *B. lanuginosum* the branch traces in fertile spike as well as pinnae arise extra-marginally.

Although Bower calls attention to the advantage of the extra-marginal method in a large and elaborate leaf, no attempt is made to show how the method may have originated. In view of the many primitive features found in *Ophioglossales* it is not surprising that certain appearances occur which may represent initial stages in the replacement of the marginal method by the extra-marginal. These have been referred to in the paper of 1910, and in the present study numerous additional series have been prepared in order to check the earlier observations. It should be borne in mind that the origin of the pinna trace in *Botrychium* is not so obvious as in some other ferns such as *Todea barbara*, where a pinna trace arises near the "hook" at one

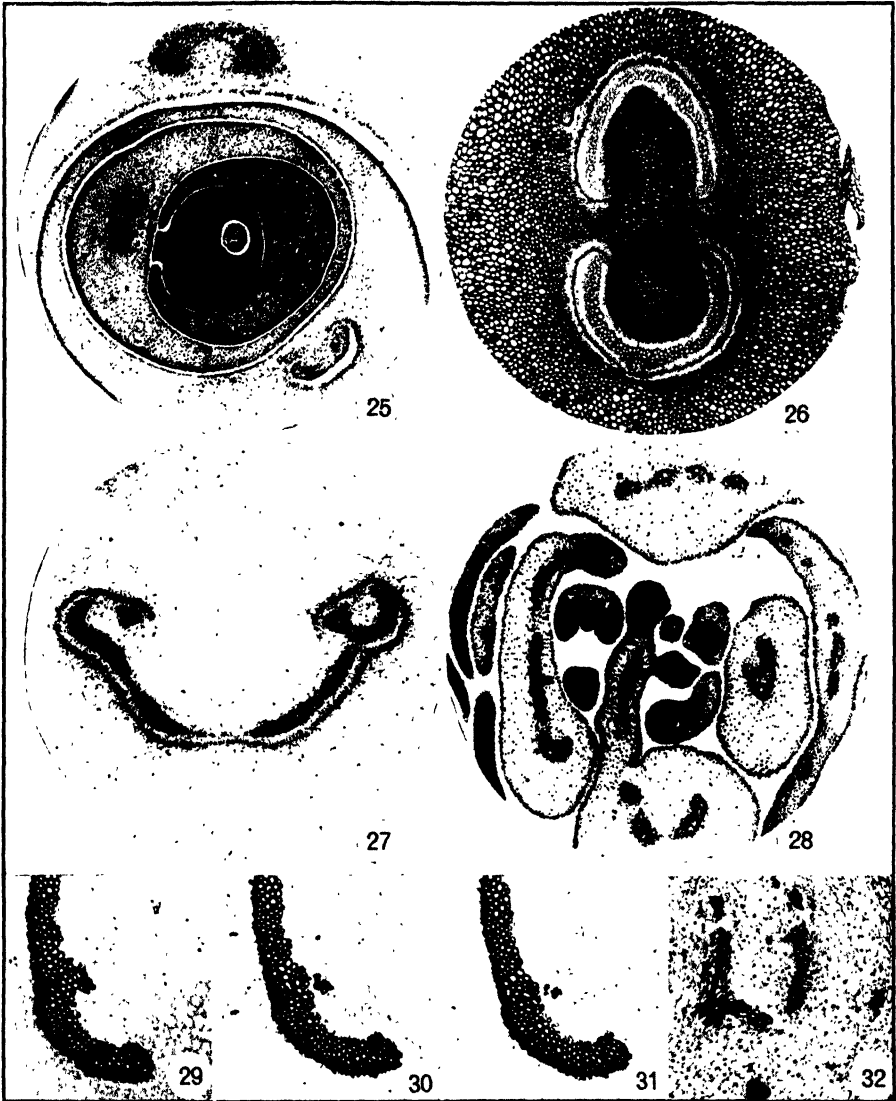


FIG. 25. *B. dissectum*: bud showing five successive leaf bases.  $\times 11$ . FIG. 26. *Adiantum pedatum*: rhizome showing dichotomy of vascular system at origin of a leaf trace (above).  $\times 15$ . FIG. 27. *B. multifidum*: fertile branch at origin of lateral branches which arise in the extra-marginal method.  $\times 25$ . FIG. 28. *B. matricariaefolium*: bud above separation of the sterile branch (above) and fertile branch (below), also vascular supply to several sporangia.  $\times 16$ . FIGS. 29-31. *B. dissectum*, large plant: edge of C-shaped petiolar bundle just below level of separation of one of the branch bundles supplying the fertile part of leaf (cf. fig. 15); figure 29 is uppermost of the series. See text.  $\times 26$ . FIG. 32. *Ophioglossum Engelmanni*, rhizome: from upper side of the stele arises a double leaf trace. At lower right appear the two parts of a lower leaf trace.  $\times 28$ .

side of the C-shaped petiolar trace, leaving a wide gap (Chrysler 1910, fig. 17). In *Botrychium virginianum* the trace arises from the abaxial side of a rather long gap, so that, following a series upward, the appearance presented is that of a small strand branching off from an adaxial edge or hook of the C (Bower 1926, vol. 2, p. 64, also figure 27 of the present paper), swinging around as it rises near the inner face of the C, eventually approaching this and fusing with it at a region somewhat removed from the margin; from this region the bundle constituting the pinna trace now breaks loose and the small marginal strand again becomes the marginal hook of the C. In 1910 I observed that in some of the smaller pinnae of *B. multifidum* (so-called *B. ternatum*) only the upper part of the marginal bundle is present—at the point on the C at which a pinna trace breaks loose a small strand is seen attached on the inner (adaxial) face of the bundle (fig. 29), and a little further down separates, running downward for a short but variable distance, dwindling (figs. 30, 31) and eventually disappearing. Such a strand was in 1910 interpreted as a vestigial structure, for the reason that because of its lack of attachment at its lower end it could not function as a conducting organ. Many additional instances have lately been observed in the fertile and sterile segments in *Sceptridium*, including one instance (mentioned in the preceding paragraph) where each of the two main bundles supplying the fertile spike arises in the manner just described. It is of interest to report also one similar case in the fertile segment of *B. lanceolatum* var. *angustisegmentum*.

But may it not be that these apparent “vestiges” on the contrary represent initial stages in the evolution of the extra-marginal method? At the point where a marginal strand is about to break off it is apt to be distinctly curved, so that a thickening is manifest where the separation occurs; this thickening may be the first step leading to the extra-marginal method. Then might follow the separation of a few tracheids from this thickened region, and the initials of such a group of tracheids might extend downward and at a later stage join the margin of the parent bundle. If this sequence appears fanciful, there are just two other possible modes of origin of the extra-marginal method that occur to the writer; either the pinna trace moved gradually from the margin toward the median region of the parent bundle, or else the new place of origin was assumed as a straight mutation. Perhaps, after all, the observations recorded in the preceding paragraph are best regarded as vestiges. But such a point of view would imply that the large-leaved species are the primitive members of the genus; this would indicate that *B. virginianum*, in which the extra-marginal plan extends to the base of the fertile spike, is the most primitive, that is, we would continue to look for ancestral conditions among the most fern-like species, which I believe is the fundamental objection to the concept of Roeper (1859), who, it will be

recalled, homologized the fertile spike with the two basal pinnae of a fern. It is probable that with Bower (1935, p. 363) we should look for the ancestors of *Ophioglossales* "among those early vascular plants in which the morphological differentiation is less determinate."

In considering these possibilities much appears to depend on whether segregation of fertile from sterile telomes occurred before or after dorsiventrality became established. If this segregation took place at an early stage in the evolution of the genus *Botrychium* we may regard the smaller degree of dorsiventrality (internal as well as external) in the fertile branch as the persistence of an ancestral feature; later the divisions of the sterile mesomes

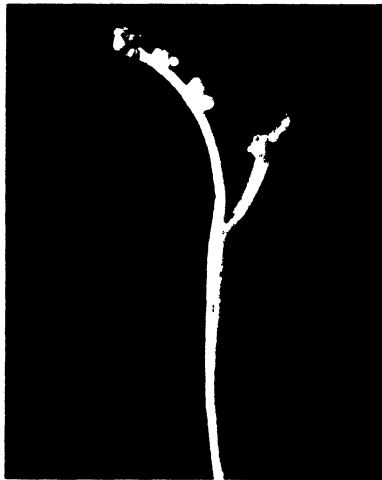


FIG. 33. *B. simplex* var. *tenebrosum*, abnormal plant. At the right is slightly flattened "sterile" branch bearing five sporangia. Natural size.

became restricted to a single plane, and an efficient photosynthetic organ arose. But if on the other hand dorsiventrality of a shoot consisting of both fertile and sterile telomes appeared at an early period, segregation of two basal branches as spore-bearing organs might follow, as appears to have taken place in *Anemia*. In such an event these two branches would have fused to make the fertile spike, while according to the other alternative the two halves of the fertile region failed to separate.

As to the cases of sporangia on branches of the sterile segment, these are of frequent occurrence in many of the species. The easiest way to interpret these cases is to consider them as reminders of the condition when there was not the sharp segregation into sterile and fertile telomes which now characterizes the order. A particularly interesting example which has come to my attention was collected in Passaic County, N. J., and is probably to be regarded as *B. simplex* var. *tenebrosum* (fig. 33). The "sterile" branch is

small, somewhat fan-shaped, and bears five relatively large sporangia in marginal position; a notch at the tip carries out the plan of a series of dichotomies as does the venation. The fertile branch shows the usual axis (fused telomes), and bears 15 sporangia, each terminating a short telome. This branch, like the sterile segment, has a terminal notch; thus the right and left parts of each branch are indicated. The plant is strangely suggestive of how an ancestral *Botrychium* may have appeared.

#### SUMMARY

1. Zimmermann has advanced the hypothesis that the fertile spike in Ophioglossales, namely, a branch arising in a plane perpendicular to that of the other divisions, represents a survival of the type of branching found in *Rhynia* and Coenopteridales. This proposal is here tested from the standpoint of vascular anatomy.

2. In subgenus *Eubotrychium* the vascular system of the shoot undergoes a series of four dichotomies in planes radial and tangential alternating with each other. At the third division the fertile and sterile branches separate. With the fourth division dorsiventrality of each branch is established, and subsequent dichotomies are in the same plane.

3. Subgenus *Sceptridium* shows less uniformity and follows one or another of three plans. Generally the second dichotomy (splitting of the leaf-trace) is absent, but transitions occur to the condition typical of *Eubotrychium*. Two possible interpretations are submitted, both in terms of dichotomy; according to the preferred interpretation, the condition in *Sceptridium* is derived from that found in *Eubotrychium*.

4. In both *Sceptridium* and *Osmundopteris* the extra-marginal origin of branch bundles obscures the dichotomous plan, and is regarded as a derived condition.

5. A possible transition from the marginal to extra-marginal mode of origin of branch bundles is described.

6. The bearing of abnormal individuals on the general problem is briefly considered.

7. The possibility of deriving Ophioglossales more or less directly from Psilophytales receives some support from the present investigation. If the evidence should be held sufficient, the hypothesis of Roeper would be abandoned.

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## THE BRYOPHYTES OF SHENANDOAH NATIONAL PARK, VIRGINIA

IRMA SCHNOOBERGER AND FRANCES E. WYNNE

In June 1944 the authors spent three weeks in Shenandoah National Park, Virginia, in the northern section of the Blue Ridge Mountains, collecting bryophytes. The living quarters used were five Appalachian Trail Club shelters (Range View, Meadow Spring, Rock Spring, Pocosin, and Doyle River) and the collections center around those regions. The areas collected are arranged below from north to south and are cited in that order in the annotated list of species concluding this report.

Little Devils Stairs, Rappahannock County. Altitude 2500-1500 feet. June 20, 1944.

Bear Wallow, Page County. Altitude 3000 feet. June 18, 1944.

Appalachian Trail south of Elk Wallow Gap, Page and Rappahannock Counties. Altitude about 2500 feet. June 19, 1944.

Buck Hollow Trail, Rappahannock County. Altitude 1500-3000 feet. June 13, 1944.

Pinnacle Ridge, Rappahannock County. Altitude 3400-3500 feet. June 14, 1944.

Limberlost, Madison County. Altitude 3200 feet. June 17, 1944.

Old Rag Mountain, Madison County. Altitude 3200 feet. June 17, 1944.

Hawksbill Mountain, Page County. Altitude 3500-4049 feet. June 16, 1944.

Appalachian Trail between Franklin Cliffs and Crescent Rocks, Page County. Altitude 3000-3500 feet. June 15-16, 1944.

Fisher's Gap and Rose River, North Fork, Madison County. Altitude 2500 feet. June 15, 1944.

Appalachian Trail—Pocosin Shelter to Lewis Mountain, Greene County. Altitude 3000-3500 feet. June 23, 1944.

Pocosin Fire Road, Greene County. June 24-25, 1944.

Appalachian Trail—Pocosin Shelter to South River, Greene County. Altitude 300-3500 feet. June 22, 1944.

South River, Greene County. Altitude 3000-2000 feet. June 22-24, 1944.

Big Flat Mountain (altitude 3600 feet), Loft Mountain (altitude 3500 feet), and Ivy Creek (altitude 2500-2000 feet), June 26, 1944.

Doyle River (altitude 3000-1600 feet) and Jones Run (altitude 1500-2800 feet), Albemarle County. June 27, 1944.

Big Run Trail, Rockingham County. Altitude 2750-1500 feet. June 29, 1944.

Big Run Bridge, Rockingham County. June 29, 1944.

All the species reported here were collected along the ridge, and none are from the valleys to the east (the Piedmont) or west (the Great Valley). The Blue Ridge is the exposed core of a large anticline composed of Pre-Cambrian igneous rocks: gneiss, schist, granite, metabasalt. The flanks of the ridge are silicious sedimentary rocks of lower Cambrian sandstone, quartzite, and some slate. The most resistant rocks of the ridge, metabasalt or greenstone, have formed the high ledges projecting several hundred feet above the summit peneplain (3500 feet elevation) and bold monadnocks such as Stony Man (4011 feet) and Hawksbill (4049 feet).



The present ridge has been produced by four periods of erosion alternated with periods of uplift. The remains of three peneplains are apparent as a result of this process and the present valley floor to the west of the Ridge is the product of the present or fourth erosion period. The sedimentary rocks including all the sandstones and limestones which once covered the ridge have been eroded away leaving only the highly resistant igneous core as the present ridge.

The result of these four extended periods of erosion is a highly dissected area with few elevated flat lands. There are few swampy areas, and therefore a limited range of habitats and a restricted diversity of flora. The region is remarkably well drained, with only two small areas which might be called swamps—one in Bear Wallow and the other at Big Meadows. This means that habitats for many aquatic or semi-aquatic bryophytes are lacking in the Park.

The fact that all the rocks in the ridge are igneous eliminates the possibility of finding several score of limestone-inhabiting bryophytes that would normally be expected to occur in the range. Comparison with the only recent extensive study of mosses in Virginia (Patterson 1940a,b, 1943, 1944) shows about 20 species occurring exclusively on limestone at Mountain Lake, Virginia; of these species only three (*Encalypta streptocarpa*, *Barbula unguiculata*, and *Anomodon viticulosus*) were found in Shenandoah National Park. Only one list of Virginia mosses (Britton 1893) had been published previous to Patterson's work.

The flora of the Blue Ridge is more closely allied with the flora of north-eastern North America than with that of the southern part of the continent. Less than ten per cent of the species found in the park are characteristically southern with their northern limit of range in Virginia. Over ninety per cent of all the bryophytes collected are species common in and characteristic of the area from New England to the Great Lakes and the Appalachians.

In the complete lists of 38 species of Hepaticae and 171 species of Musci, which form the main body of this paper, rare species and range extensions are marked with an asterisk. The most interesting mosses and liverworts are listed immediately below with the known range in North America and the adjoining states as given for West Virginia by Ammons (1940) and Tennessee by Sharp (1939).

### Hepaticae

*PTILIDIUM CILIARE*. Greenland to Alaska, south to New England and Minnesota. Not reported in West Virginia, Virginia, or Tennessee.

*CEPHALOZIELLA HAMPEANA*. Widespread but not collected in West Virginia, Virginia, Tennessee, or in Virginia since 1892 (Haynes 1927).

*LOPHOCOLEA MINOR*. Quebec to British Columbia, south to Pennsylvania, Indiana, Kentucky, West Virginia, Minnesota, Montana, Idaho, and New Mexico. Not reported in Tennessee or by Sharp (1944) in Virginia; collected once in Virginia by Small (Evans 1893).

*CHILOSCYPHUS PALLESCENS*. Quebec to British Columbia, south to North Carolina, Kentucky, Tennessee, Idaho, New Mexico, Utah, Oregon, Washington. Not before reported in Virginia. This species was found also near the park headquarters just outside the park boundary.

*CHILOSCYPHUS POLYANTHUS*. Labrador to Alaska, south to North Carolina, Tennessee, Missouri, Colorado, Utah, and California. Not collected in Virginia since 1892 (Haynes 1927).

*CHILOSCYPHUS RIVULARIS*. Newfoundland to British Columbia, south to North Carolina, Oklahoma, New Mexico, and California. Not reported in Virginia since 1937 (Bloomquist).

*BARBILOPHOZIA BARBATA*. Greenland to Yukon, south to New York, New Jersey, and Virginia. Reported by Sharp (1944) as rare at Mountain Lake.

*PLAGIOCHILA LUDOVICIANA*. Sharp (1944) says of this species, "This rather robust hepatic has not been reported before north of Tennessee and North Carolina." The present specimen from Shenandoah National Park extends the range farther north in Virginia.

### Musci

The following species and varieties are believed to be new to Virginia:

*FISSIDENS VIRIDULUS*. South to the middle Atlantic states; rare in Tennessee.

*DITRICHUM LINEARE*. Prince Edward Island to S. Carolina and Missouri. Rare in Tennessee.

*DICRANOWEISIA CRISPULA*. Greenland to Labrador, Mt. Marcy, N. Y., and Mt. Katahdin, Maine.

*DICRANELLA VARIA*. Not common in Tennessee.

*RHACOMITICUM HETEROSTICHUM* var. *GRACILESCENS* Bry. Eur. "Apparently very rare but your specimen checks with *Holzinger 186*, cited as the first American collection," Geneva Sayre.

*MNIUM ORTHORHYNCHUM*. In the east, south to North Carolina.

*THUIDIUM PHILIBERTI*. Southern Canada, south to Pennsylvania, New Jersey, and New Mexico.

*BRACHYTHECIUM RUTABULUM*. Northern North America, south to New Jersey and Pennsylvania; rare in Tennessee.

*BRACHYTHECIUM VELUTINUM*. Northern North America, south to New Jersey.

*CHAMBERLAINIA BIVENTROSA*. Known only from Louisiana.

*SEMATOPHYLLUM CAESPITOSUM*. Rare in Florida.

*HYPNUM PALLESCENS*. Northern North America, south in the mountains to Tennessee; rare in Tennessee.

*HYLOCOMIUM UMBRATUM*. Northern North America, south in the mountains to North Carolina; rare in Tennessee.

*POLYTRICHUM PILIFERUM*. Northern North America, south to New Jersey; rare in Tennessee.

### ACKNOWLEDGMENTS

The authors wish to express their appreciation to Dr. E. H. Walker who gave valuable advice in planning the trip, to the Potomac Appalachian Trail Club for the use of their facilities in the Park, to Mr. E. H. Freeland, Super-

intendent of the Park and Mr. W. T. Stephens, Head Ranger, for their valuable assistance and cooperation in Shenandoah National Park.

Identifications have been made by the authors and Dr. Margaret Fulford (Hepaticae), Dr. Winona H. Welch (Frontinalaceae), and Dr. Geneva Sayre (Grimmiaceae). Dr. W. C. Steere has kindly checked doubtful species.

Specimens are deposited in the writers' private herbaria, at Shenandoah National Park, the New York Botanical Garden, and the University of Michigan Herbarium.

In the list of species the nomenclature and arrangement follow Brotherus in the second edition of Engler & Prantl's *Die Natürlichen Pflanzenfamilien* for the Musei and Evans' "List of Hepaticae Found in the United States, Canada, and Arctic America" for the Hepaticae.

### HEPATICAE

#### PTILIDIACEAE

\**PTILIDIUM CILIARE* (L.) Nees. Little Devils Stairs, Lewis Mountain, Ivy Creek, Doyle River. Morphologically these plants fit the description of *P. ciliare*, but their habitat was not typical. These were collected on logs, whereas *P. ciliare* typically grows on rocks. It is interesting that Sharp (1944) reports *P. pulcherrimum* on rocks instead of its usual substratum of rotten logs.

*PTILIDIUM PULCHERRIMUM* (Web.) Hampe. Buck Hollow, Jones Run.

#### LEPIDOZACEAE

*MICROLEPIDOZIA SYLVATICA* (Evans) Joerg. Big Run Bridge.

#### CEPHALOZACEAE

*CEPHALOZIA CONNIVENS* (Dicks.) Lindb. Big Run.

*NOWELLIA CURVIFOLIA* (Dicks.) Mitt. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Franklin Cliffs to Crescent Rocks, Rose River, Lewis Mountain, South River, Ivy Creek, Jones Run.

*ODONTOSCHISMA DENUDATUM* (Mart.) Dumort. Bear Wallow, Elk Wallow Gap, Ivy Creek, Jones Run.

#### CEPHALOZIELLIACEAE

\**CEPHALOZIELLA HAMPEANA* (Nees) Schiffn. Little Devils Stairs, Big Run.

#### HARPANTHACEAE

*LOPHOCOLEA BIDENTATA* (L.) Dumort. Bear Wallow.

*LOPHOCOLEA HETEROPHYLLA* (Schr.) Dumort. Little Devils Stairs, Buck Hollow, Pinnacle Ridge, South River, Ivy Creek.

\**LOPHOCOLEA MINOR* Nees. Ivy Creek.

\**CHIOSCYPHUS POLYANTHUS* (L.) Corda. Big Run.

\**CHIOSCYPHUS PALLESCENS* (Ehrh.) Dumort. Buck Hollow.

\**CHIOSCYPHUS RIVULARIS* (Schr.) Loeske. Ivy Creek. Bloomquist (1937) records *C. rivularis* for Mountain Lake, but Sharp (1944) did not collect it again.

## JUNGERMANNIACEAE

\**BARBILOPHOZIA BARBATA* (Schmid.) Loeske. Pinnacle Ridge, Big Run.  
*JAMESONIELLA AUTUMNALIS* (DC.) Steph. Little Devils Stairs, Buck Hollow, South River, Lewis Mountain, Pocosin to South River.

*PLECTOCOLEA CRENULATA* (Smith) Evans. Little Devils Stairs, Ivy Creek, Big Flat Mountain, Big Run.

## MARSUPELLACEAE

*MARSUPELLA EMARGINATA* (Ehrh.) Dumort. Hawksbill, Franklin Cliffs, Rose River, Pocosin Fire Road, South River, Big Run.

## PLAGIOCHILACEAE

*PLAGIOCHILA ASPLENIODES* (L.) Dumort. Little Devils Stairs, Buck Hollow, Jones Run, Doyle River.

\**PLAGIOCHILA LUDOVICIANA* Sulliv. Little Devils Stairs. Sharp (1944) first reported this species in Virginia, unknown previously north of Tennessee and North Carolina. This collection extends its range farther north in Virginia.

## SCAPANIACEAE

*DIPLOPHYLLUM APICULATUM* (Evans) Steph. Hawksbill, Franklin Cliffs.

*SCAPANIA NEMOROSA* (L.) Dumort. Little Devils Stairs, Bear Wallow, Buck Hollow, Hawksbill, Franklin Cliffs to Crescent Rocks, Rose River, South River, Pocosin to South River, Ivy Creek, Big Run, Big Run Bridge.

*SCAPANIA UNDULATA* (L.) Dumort. Bear Wallow, Buck Hollow.

## PORELLACEAE

*PORELLA PINNATA* L. Bear Wallow, Buck Hollow.

*PORELLA PLATYPHYLLOIDEA* (Schwein.) Lindb. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Hawksbill, Franklin Cliffs, Lewis Mountain, South River, Doyle River.

## RADULACEAE

*RADULA COMPLANATA* (L.) Dumort. Little Devils Stairs, Buck Hollow.

*RADULA OBCONICA* Sulliv. Buck Hollow.

## FRULLANIACEAE

*FRULLANIA ASAGRAYANA* Mont. Little Devils Stairs, Buck Hollow, Hawksbill, Rose River, Limberlost, Lewis Mountain, South River, Pocosin to South River, Big Run.

*FRULLANIA BRITTONIAE* Evans. Buck Hollow, Pinnacle Ridge, Hawksbill, Lewis Mountain.

*FRULLANIA EBORACENSIS* Gottsche. Little Devils Stairs, Buck Hollow, Pinnacle Ridge, Limberlost, Old Rag, Big Meadows, Hawksbill, Rose River, Lewis Mountain, South River, Big Run.

*FRULLANIA RIPARIA* Hampe. Ivy Creek, Doyle River, Jones Run.

*JUBULA PENNSYLVANICA* (Steph.) Evans. Little Devils Stairs, Elk Wallow, Buck Hollow, Rose River.

## LEJEUNEACEAE

LEUCOLEJEUNEA CLYPEATA (Schwein.) Evans. Buck Hollow, Rose River, Doyle River.

LEJEUNEA CAVIFOLIA (Ehrh.) Lindb. Little Devils Stairs, Buck Hollow, Franklin Cliffs.

LEJEUNEA PATENS Lindb. Little Devils Stairs, Buck Hollow, Doyle River.

## METZGERIACEAE

METZGERIA CONJUGATA Lindb. Buck Hollow, Doyle River.

METZGERIA CRASSIPILIS (Lindb.) Evans. South River, Doyle River, Jones Run.

## MARCHANTIACEAE

CONOCEPHALUM CONICUM (L.) Dumort. Little Devils Stairs, Ivy Creek.

## REBOULIACEAE

REBOULIA HEMISPHERICA (L.) Raddi. South River.

## MUSCI

## ANDREAEEAE

ANDREAEA ROTHII Web. & Mohr. Hawksbill.

## FISSIDENTACEAE

FISSIDENS ADIANTOIDES Hedw. Little Devils Stairs, Bear Wallow, Buck Hollow, Franklin Cliffs, Jones Run.

FISSIDENS CRISTATUS Wils. Little Devils Stairs, Bear Wallow, Buck Hollow, Franklin Cliffs, Pocosin Shelter to South River, South River, Pocosin Fire Road, Ivy Creek, Doyle River, Jones Run, Big Run.

FISSIDENS MINUTULUS Sull. Elk Wallow, Buck Hollow, Rose River, Old Rag, Ivy Creek, Doyle River.

FISSIDENS OSMUNDIODES Hedw. Bear Wallow, Buck Hollow, Franklin Cliffs, Pocosin Fire Road, South River, Loft Mountain, Doyle River, Big Run.

FISSIDENS SUBBASILARIS Hedw. Buck Hollow, Limberlost, Lewis Mountain.

FISSIDENS TAXIFOLIUS Hedw. Bear Wallow, Rose River, South River, Lewis Mountain, Big Run.

\*FISSIDENS VIRIDULUS (Web. & Mohr) Wahlenb. Pocosin to South River, South River, Ivy Creek.

## DITRICHACEAE

CERATODON PURPUREUS (Hedw.) Brid. Little Devils Stairs, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Hawksbill, Pocosin Fire Road, South River, Lewis Mountain, Big Flat Mountain.

\*DITRICHUM LINEARE (Sw.) Lindb. Hawksbill, Jones Run.

DITRICHUM PALLIDUM (Hedw.) Hampe. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Rose River, Hawksbill, Old Rag, Loft Mountain, Ivy Creek, Doyle River, Big Run.

DITRICHUM PUSILLUM (Hedw.) E. G. Britton. Little Devils Stairs, Elk Wallow Gap, Pinnacle Ridge, Franklin Cliffs, Hawksbill, Rose River, South River, Lewis Mountain, Big Flat Mountain, Ivy Creek, Big Run.

## DICRANACEAE

*DICRANELLA HETEROMALLA* (Hedw.) Schimp. Elk Wallow Gap, Pinnacle Ridge, Hawksbill, Limberlost, Old Rag, Fishers Gap, Lewis Mountain, Pocosin to South River, Loft Mountain, Jones Run, Big Run.

\**DICRANELLA VARIA* (Hedw.) Schimp. Elk Wallow Gap, Pocosin Fire Road.

\**DICRAONOWEISIA CRISPULA* (Hedw.) Lindb. Pinnacle Ridge, Hawksbill, Ivy Creek.

*PARALEUCOBRYUM LONGIFOLIUM* (Hedw.) Loeske. Elk Wallow Gap.

*RHADBOWEISIA DENTICULATA* (Brid.) Bry. Eur. Old Rag, Franklin Cliffs, Crescent Rocks.

*DICRANUM BONJEANI* DeNot. Franklin Cliffs.

*DICRANUM FLAGELLARE* Hedw. Bear Wallow, Elk Wallow Gap, Buck Hollow, Rose River, South River, Ivy Creek, Loft Mountain.

*DICRANUM FULVUM* Hook. Little Devils Stairs, Bear Wallow, Buck Hollow, Hawksbill, Rose River, Franklin Cliffs, Big Meadows, Pocosin Fire Road, South River, Lewis Mountain, Ivy Creek, Big Run.

*DICRANUM FUSCESCENS* Turn. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Hawksbill, Franklin Cliffs, Rose River, Old Rag, Pocosin Fire Road, South River, Ivy Creek, Big Run.

*DICRANUM MONTANUM* Hedw. Little Devils Stairs, Buck Hollow, Limberlost, Pocosin Fire Road, South River, Lewis Mountain, Doyle River.

*DICRANUM RUGOSUM* (Hoffm.) Brid. Franklin Cliffs.

*DICRANUM SCOPARIUM* Hedw. Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Hawksbill, Franklin Cliffs, Rose River, Pocosin Fire Road, South River, Lewis Mountain, Doyle River, Big Run.

## LEUCOBRYACEAE

*LEUCOBRYUM ALBIDUM* (Brid.) Lindb. Bear Wallow, Lewis Mountain, Big Run.

*LEUCOBRYUM GLAUCUM* (Hedw.) Schimp. Bear Wallow, Elk Wallow Gap, Buck Hollow, Franklin Cliffs, Rose River, Limberlost, Pocosin Fire Road, South River, Ivy Creek, Doyle River, Big Run, Big Run Bridge.

## ENCALYPTACEAE

*ENCALYPTA STREPTOCARPA* Hedw. Pocosin Shelter to South River, Drive at Big Run Trail.

## POTTIACEAE

*WEISIA VIRIDULA* Hedw. Pocosin Shelter to South River, Doyle River, Big Run.

*TORTELLA CAESPITOSA* (Schwaegr.) Limpr. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Franklin Cliffs, Rose River, Pocosin Shelter to South River, Jones Run, Doyle River, Big Run.

*BARBULA UNGUICULATA* Hedw. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Pocosin Fire Road, South River, Ivy Creek, Doyle River, Big Run.

## GRIMMIACEAE

*GRIMMIA ALPICOLA* var. *RIVULARIS* (Brid.) Broth. Buck Hollow, Old Rag, Rose River.

GRIMMIA APOCARPA Hedw. Pocòsin to South River, Doyle River.

GRIMMIA APOCARPA var. CONVERTA (Funck.) Spreng. Crescent Rocks.

GRIMMIA APOCARPA var. GRACILIS (Schleich.) W. & M. Big Run.

GRIMMIA PILIFERA Beauv. Elk Wallow Gap, Little Devils Stairs, Pinnacle Ridge, Limberlost, Lewis Mountain, Doyle River, Big Run.

\*RHACOMITRIUM HETEROSTICHUM var. GRACILESCENS Bry. Eur. Crescent Rocks.

#### FUNARIACEAE

PHYSCOMITRIUM TURBINATUM (Michx.) Brid. Buck Hollow, Pocòsin Shelter to South River, Doyle River.

#### TETRAPHIDACEAE

TETRAPHIS PELLUCIDA Hedw. Little Devils Stairs, Bear Wallow, Rose River, Big Run Bridge.

#### BRYACEAE

MNIOBRYUM ALBICANS (Wahlenb.) Limpr. [*Pohlia Wahlenbergii* (Web. & Mohr) Andrews]. Buck Hollow, Big Run.

BRYUM ARGENTEUM Hedw. Bear Wallow, Buck Hollow, Pinnacle Ridge, Lewis Mountain.

BRYUM BIMUM Schreb. Little Devils Stairs, Bear Wallow, Buck Hollow, Hawksbill, Franklin Cliffs, Rose River, Lewis Mountain, Pocòsin Shelter to South River, Doyle River, Jones Run.

BRYUM CAESPITICIUM Hedw. Little Devils Stairs, Buck Hollow, Pinnacle Ridge, Lewis Mountain, Ivy Creek, Jones Run.

BRYUM CAPILLARE Hedw. Little Devils Stairs, Pinnacle Ridge, Old Rag, Franklin Cliffs, Pocòsin Shelter to South River, Doyle River, Big Run.

RHODOBRYUM ROSEUM (Bry. Eur.) Limpr. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Pinnacle Ridge, Old Rag, Hawksbill, Rose River, Pocòsin Shelter to South River, Pocòsin Fire Road, South River, Lewis Mountain, Jones Run, Big Run.

POHLIA CRUDA (Hedw.) Lindb. Lewis Mountain.

POHLIA NUTANS (Schreb.) Lindb. Buck Hollow.

MNIUM AFFINE Bland. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Hawksbill, Franklin Cliffs, Pocòsin Fire Road, Pocòsin Shelter to South River, South River, Lewis Mountain, Ivy Creek, Doyle River, Big Run.

MNIUM CUSPIDATUM Hedw. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Pinnacle Ridge, Hawksbill, Pocòsin Shelter to South River, South River, Doyle River, Jones Run, Big Run.

MNIUM HORNUM Hedw. Buck Hollow, Big Run Bridge.

MNIUM MARGINATUM (Dicks.) P. B. Little Devils Stairs.

\*MNIUM ORTHORHYNCHUM Brid. Little Devils Stairs.

MNIUM PUNCTATUM Hedw. Little Devils Stairs, Buck Hollow, Pinnacle Ridge, Rose River, Ivy Creek.

MNIUM STELLARE Reich. Jones Run.

#### AULACOMNIACEAE

AULACOMNIUM HETEROSTICHUM (Hedw.) Bry. Eur. Little Devils Stairs, Elk Wallow Gap, Franklin Cliffs, Pocòsin Shelter to South River, Doyle River, Jones Run, Big Run.

*AULACOMNIUM PALUSTRE* (Web. & Mohr) Schwaegr. Little Devils Stairs, Buck Hollow, Pinnacle Ridge.

#### BARTRAMIACEAE

*BARTRAMIA POMIFORMIS* Hedw. Elk Wallow Gap, Buck Hollow, Franklin Cliffs, Hawksbill, Pocosin Shelter to South River, South River, Jones Run, Big Run.

\**PHILONOTIS AMERICANA* Dismier. Big Run Bridge.

*PHILONOTIS FONTANA* (Hedw.) Brid. Little Devils Stairs, Bear Wallow, Buck Hollow, Pinnacle Ridge, Franklin Cliffs, Pocosin Shelter to South River, South River, Doyle River.

#### ORTHOTRICACEAE

*ORTHOTRICHUM OHIOENSE* Sull. & Lesq. Loft Mountain.

\**ORTHOTRICHUM SPECIOSUM* Nees. Pinnacle Ridge, Old Rag, Big Run.

*ULOTA AMERICANA* (P. B.) Limpr. Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Limberlost, Old Rag, Hawksbill, Franklin Cliffs, Rose River, Pocosin Fire Road, South River, Lewis Mountain, Ivy Creek, Big Run.

*ULOTA CRISPA* (Hedw.) Brid. Little Devils Stairs, Limberlost, Old Rag, Big Meadows, Hawksbill, Rose River, Lewis Mountain, Pocosin Shelter to South River, Big Flat Mountain, Loft Mountain, Big Run.

*DRUMMONDIA PROREPENS* (Hedw.) Jenn. Little Devils Stairs, Pinnacle Ridge, Hawksbill, Crescent Rocks, Lewis Mountain, Pocosin Shelter to South River, Big Flat Mountain, Loft Mountain, Ivy Creek, Jones Run, Big Run.

#### FONTINALACEAE

*FONTINALIS NOVAE-ANGLIAE* Sull. Bear Wallow.

#### CLIMACIACEAE

*CLIMACIUM AMERICANUM* Brid. Bear Wallow, Buck Hollow, Pocosin Shelter to South River, Big Flat Mountain, Ivy Creek, Doyle River, Jones Run, Big Run Bridge.

*CLIMACIUM DENDROIDES* (Hedw.) Web. & Mohr. Pocosin Shelter to South River, Doyle River.

*CLIMACIUM KINDBERGII* (R. & C.) Grout. Big Run Bridge.

*POROTRICHUM ALLEGHANIENSE* (C. Müll.) Grout. Little Devils Stairs, Buck Hollow, Pocosin Shelter to South River, Lewis Mountain, Jones Run.

#### HEDWIGIACEAE

*HEDWIGIA CILIATA* Hedw. Little Devils Stairs, Bear Wallow, Buck Hollow, Pinnacle Ridge, Old Rag, Hawksbill, Franklin Cliffs, Rose River, Pocosin Shelter to South River, Lewis Mountain, Ivy Creek, Big Run.

#### LEUCODONTACEAE

*LEUCODON BRACHYPUS* Brid. Hawksbill, Franklin Cliffs, Rose River, Pocosin Fire Road, South River, Big Flat Mountain, Big Run.

*LEUCODON JULACEUS* f. *FLAGELLIFERUS* Grout. Ivy Creek.

*LEUCODON SCIUROIDES* (Hedw.) Schwaegr. Pinnacle Ridge, Limberlost, Old Rag.



*LEPTODON TRICHOMITRIUM* (Hedw.) Mohr. Buck Hollow, Rose River, Lewis Mountain, Pocosin Shelter to South River, South River, Doyle River.

#### NECKERACEAE

*NECKERA PENNATA* Hedw. Rose River, Ivy Creek.

#### THELIACEAE

*THELIA ASPRELLA* (Hedw.) Sull. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Hawksbill, Franklin Cliffs, Lewis Mountain, Pocosin Shelter to South River, South River, Doyle River, Big Run.

*THELIA HIRTELLA* (Hedw.) Sull. Elk Wallow Gap.

#### FABRONIACEAE

*SCHWETSCHKEOPSIS DENTICULATA* (Sull.) Broth. Little Devils Stairs, Rose River, Pocosin Shelter to South River, Big Run.

#### LESKEACEAE

*LESKEA OBSCURA* Hedw. Rose River, Big Flat Mountain.

*LESKEA POLYCARPA* (Ehrh.) Hedw. Hawksbill, Lewis Mountain, Pocosin Shelter to South River, Doyle River.

#### THUIDIACEAE

*ANOMODON ATTENUATUS* (Hedw.) Hueben. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Limberlost, Old Rag, Franklin Cliffs, Rose River, Big Meadows, Lewis Mountain, Pocosin Shelter to South River, Doyle River, Big Run.

*ANOMODON MINOR* (P. B.) Lindb. Pinnacle Ridge, Limberlost, Lewis Mountain, Pocosin Shelter to South River, South River, Doyle River, Jones Run.

*ANOMODON ROSTRATUS* (Hedw.) Schimp. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Rose River, Pocosin Fire Road, South River, Doyle River, Jones Run, Big Run.

*ANOMODON RUGELII* (C. Müll.) Keissl. Pinnacle Ridge, Crescent Rocks, Rose River, Lewis Mountain, Big Flat Mountain.

*ANOMODON TRISTIS* (Cesati) Sull. Pinnacle Ridge, Big Flat Mountain.

*ANOMODON VITICULOSUS* (Hedw.) Hook. & Tayl. Buck Hollow, Old Rag, Hawksbill, Franklin Cliffs, Rose River, Pocosin Shelter to South River, Doyle River, Jones Run.

*THUIDIUM ABIETINUM* (Brid.) Bry. Eur. Crescent Rocks.

*THUIDIUM DELICATULUM* (Hedw.) Mitt. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Limberlost, Old Rag, Hawksbill, Franklin Cliffs, Lewis Mountain, Pocosin Fire Road, South River, Big Flat Mountain, Ivy Creek, Doyle River, Big Run.

\**THUIDIUM PHILIBERTI* Limpr. Big Run.

*THUIDIUM SCITUM* (P. B.) Aust. Bear Wallow, Elk Wallow Gap, Hawksbill, Rose River, Lewis Mountain, Pocosin Fire Road, South River, Jones Run.

*THUIDIUM RECOGNITUM* (Hedw.) Lindb. Pocosin Shelter to South River, Big Run.

*THUIDIUM VIRGINIANUM* (Brid.) Lindb. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Limberlost, Franklin Cliffs, Rose River, Lewis Mountain, Pocosin Fire Road, South River, Ivy Creek, Big Flat Mountain, Doyle River, Jones Run, Big Run.

#### AMBLYSTEGIACEAE

*CAMPYLUM CHRYSOPHYLLUM* (Brid.) Bryhn. Little Devils Stairs, Bear Wallow, Buck Hollow, Franklin Cliffs, Crescent Rocks, Pocosin Fire Road, South River, Jones Run, Big Run.

*CAMPYLUM HISPIDULUM* (Brid.) Mitt. Bear Wallow, Elk Wallow Gap, Pinnacle Ridge, Rose River, Lewis Mountain, Pocosin Shelter to South River, Big Run.

\**CAMPYLUM POLYGAMUM* (Bry. Eur.) Bryhn. Buck Hollow, South River, Doyle River.

*CAMPYLUM RADICALE* (P. B.) Grout. Bear Wallow, Rose River.

\**HYGROAMBLYSTEGIUM FLUVIATILE* (Sw.) Loeske. Doyle River.

\**HYGROAMBLYSTEGIUM FLUVIATILE* var. *OVATUM* Grout. Little Devils Stairs, Elk Wallow Gap, Buck Hollow, Crescent Rocks, Fishers Gap, Pocosin Shelter to South River, Doyle River.

*HYGROAMBLYSTEGIUM IRRIGUUM* (Wils.) Loeske. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Rose River, Pocosin Shelter to South River, South River, Ivy Creek, Doyle River, Jones Run.

*HYGROAMBLYSTEGIUM IRRIGUUM* var. *SPINIFOLIUM* (Schimp.) Grout. Little Devils Stairs, Pocosin Shelter to South River, Ivy Creek, Doyle River.

*HYGROAMBLYSTEGIUM ORTHOCLADON* (P. B.) Grout. South River, Big Run.

*SCIAROMIUM LESCURI* (Sull.) Broth. Bear Wallow, Buck Hollow, Rose River, Big Run Bridge.

*LEPTODICTYUM TRICHOPODIUM* var. *KOCHII* (Br. & Sch.) Broth. Little Devils Stairs, Big Run.

\**AMBLYSTEGIUM JURATZKANUM* Schimp. Buck Hollow, Limberlost.

*AMBLYSTEGIUM SERPENS* (Hedw.) Bry. Eur. Little Devils Stairs, Buck Hollow, Pinnacle Ridge, Big Meadows, Lewis Mountain, Pocosin Shelter to South River, Doyle River.

*AMBLYSTEGIUM VARIUM* (Hedw.) Lindb. Little Devils Stairs, Bear Wallow, Pinnacle Ridge, Old Rag, Pocosin to South River, Doyle River.

*AMBLYSTEGIELLA CONFERVOIDES* (Brid.) Loeske. Lewis Mountain.

*AMBLYSTEGIELLA SUBTILIS* (Hedw.) Loeske. Pinnacle Ridge, Rose River.

*HYGROHYPNUM DILATATUM* (Wils.) Loeske. Buck Hollow.

*HYGROHYPNUM EUGYRIUM* (Br. & Sch.) Loeske. Buck Hollow, Ivy Creek.

*PLEUROZIUM SCHREBERI* (Bry. Eur.) Mitt. Hawksbill.

#### BRACHYTHECIACEAE

*BRACHYTHECIUM ACUTUM* (Mitt.) Sull. Jones Run, Doyle River.

*BRACHYTHECIUM DIGASTRUM* C. Müll. & Kindb. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Pinnacle Ridge, Pocosin Shelter to South River, Jones Run, Big Run.

*BRACHYTHECIUM OXYCLADON* (Brid.) Jaeger & Sauerb. Little Devils Stairs, Bear Wallow, Old Rag, Franklin Cliffs, Rose River, Lewis Mountain, Pocosin Fire Road, South River, Ivy Creek, Doyle River, Jones Run, Big Run.

*BRACHYTHECIUM PLUMOSUM* (Sw.) Br. & Sch. Little Devils Stairs, Elk Wallow Gap, Buck Hollow, Hawksbill, Franklin Cliffs, Pocosin Shelter to South River, Ivy Creek, Big Run.

*BRACHYTHECIUM RIVULARE* Br. & Sch. Little Devils Stairs, Elk Wallow Gap, Buck Hollow, Rose River, Pocosin Shelter to South River, South River, Ivy Creek, Jones Run, Doyle River.

\**BRACHYTHECIUM RUTABULUM* (Hedw.) Bry. Eur. Bear Wallow, Buck Hollow, Rose River.

*BRACHYTHECIUM SALEBROSUM* (Hoffm.) Br. & Sch. Elk Wallow Gap, Buck Hollow, Old Rag, Franklin Cliffs, Pocosin Shelter to South River.

\**BRACHYTHECIUM VELUTINUM* (Hedw.) Bry. Eur. Old Rag.

*BRYHNIA GRAMINICOLOR* (Brid.) Grout. Little Devils Stairs, Pocosin Shelter to South River.

*BRYHNIA NOVAE-ANGLIAE* (Sull. & Lesq.) Grout. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Old Rag, Crescent Rocks, Pocosin Shelter to South River, Ivy Creek, Big Run.

*CIRRIPHYLLUM BOSCHII* (Schwaegr.) Grout. Bear Wallow.

*CHAMBERLAINIA ACUMINATA* (Hedw.) Grout. Rose River, Pocosin Shelter to South River, Big Run.

\**CHAMBERLAINIA BIVENTROSA* (C. Müll.) Grout. Lewis Mountain, Jones Run.

*CHAMBERLAINIA CYRTOPHYLLA* (Kindb.) Grout. Jones Run, Doyle River.

*EURHYNCHIUM HIANIS* (Hedw.) Jaeger & Sauerb. Jones Run.

*EURHYNCHIUM RUSCIFORME* (Nedk.) Milde. Little Devils Stairs, Buck Hollow, Rose River, Pocosin Shelter to South River, South River, Ivy Creek, Doyle River.

*EURHYNCHIUM SERRULATUM* (Hedw.) Kindb. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Old Rag, Franklin Cliffs, Rose River, Lewis Mountain, Pocosin Fire Road, South River, Doyle River, Big Run.

*EURHYNCHIUM STRIGOSUM* (Hoffm.) Bry. Eur. Little Devils Stairs, Elk Wallow Gap, Old Rag, Big Run.

*EURHYNCHIUM STRIGOSUM* var. *PRAECOX* (Hedw.) Husnot. Little Devils Stairs, Elk Wallow Gap.

#### ENTODONTACEAE

*ENTODON BREVISETUS* (Hook & Wils.) Jaeger & Sauerb. Lewis Mountain.

*ENTODON CLADORRHIZANS* (Hedw.) C. Müll. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Hawksbill, Franklin Cliffs, Rose River, Lewis Mountain, Pocosin Shelter to South River, Pocosin Fire Road, Big Flat Mountain, Jones Run, Big Run.

*ENTODON SEDUCTRIX* (Hedw.) C. Müll. Elk Wallow Gap, Franklin Cliffs, Crescent Rocks, Lewis Mountain, Pocosin Fire Road, Pocosin to South River, South River, Ivy Creek, Doyle River, Big Run.

#### PLAGIOTHECIACEAE

*PLAGIOTHECIUM DENTICULATUM* (Hedw.) Bry. Eur. Little Devils Stairs, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Rose River, Franklin Cliffs, Pocosin Shelter to South River, Ivy Creek, Doyle River, Big Run.

*PLAGIOTHECIUM DEPLANATUM* (Sull.) Grout. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Rose River, South River.

*PLAGIOTHECIUM ELEGANS* (Hook.) Sull. Bear Wallow, Old Rag, Franklin Cliffs, Ivy Creek.

*PLAGIOTHECIUM LAETUM* Bry. Eur. Buck Hollow, Franklin Cliffs, Pocosin Shelter to South River.

*PLAGIOTHECIUM MUELLERIANUM* Schimp. Limberlost, Pocosin Shelter to South River.

*PLAGIOTHECIUM ROSEANUM* (Hampe) Bry. Eur. Franklin Cliffs, Pocosin Shelter to South River, Jones Run.

*PLAGIOTHECIUM SYLVATICUM* (Brid.) Bry. Eur. Little Devils Stairs, Ell Wallow Gap, Buck Hollow, Rose River, Franklin Cliffs, Pocosin Shelter to South River, Doyle River, Jones Run.

*PLAGIOTHECIUM TURFACEUM* (Lindb.) Lindb. Rose River, Ivy Creek, Doyle River, Big Run.

#### SEMATOPHYLLACEAE

*HETEROPHYLLUM HALDANIANUM* (Brev.) Kindb. Buck Hollow, Pinnacle Ridge, Franklin Cliffs, Pocosin Shelter to South River, Lewis Mountain.

*BROTHERELLA DELICATULA* (James) Fleisch. Pinnacle Ridge, Franklin Cliffs.

*BROTHERELLA RECURVANS* (Michx.) Fleisch. Big Run.

\**SEMATOPHYLLUM CAESPITOSUM* (Hedw.) Mitt. Elk Wallow Gap, Rose River, Doyle River.

*SEMATOPHYLLUM CAROLINIANUM* (C. Müll.) E. G. Britton. Buck Hollow, Pinnacle Ridge, Ivy Creek.

*SEMATOPHYLLUM MARYLANDICUM* (C. Müll.) E. G. Britton. Buck Hollow.

*HOMOMALLIUM ADNATUM* (Hedw.) Broth. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Old Rag, Hawksbill, Crescent Rocks, Rose River, Lewis Mountain, Pocosin Shelter to South River, Big Flat Mountain, Ivy Creek, Doyle River, Big Run.

*HYPNUM ARCUATUM* Lindb. Bear Wallow.

*HYPNUM CUPRESSIFORME* Hedw. Bear Wallow, Buck Hollow, Rose River, Pocosin Shelter to South River, Ivy Creek, Doyle River.

*HYPNUM CURVIFOLIUM* Hedw. Bear Wallow, Buck Hollow, Rose River, Hawksbill, Franklin Cliffs, Pocosin Fire Road, South River, Ivy Creek, Jones Run.

*HYPNUM FERTILE* Sendt. Bear Wallow, Elk Wallow Gap, Hawksbill, Pocosin Fire Road, Big Run.

*HYPNUM IMPONENS* Hedw. Bear Wallow, Elk Wallow Gap, Pinnacle Ridge, Rose River, Pocosin Shelter to South River, Loft Mountain, Big Run.

*HYPNUM MOLLUSCUM* Hedw. Buck Hollow, Pinnacle Ridge.

\**HYPNUM PALLESCENS* (Hedw.) Bry. Eur. Franklin Cliffs, Pocosin Fire Road, South River, Jones Run, Doyle River, Big Run.

*HYPNUM REPTILE* Michx. Little Devils Stairs, Hawksbill, Pocosin Fire Road, South River, Big Run.

*PYLAISIA INTRICATA* (Hedw.) Bry. Eur. Bear Wallow, Old Rag, Hawksbill, Franklin Cliffs, Lewis Mountain, Pocosin Shelter to South River, South River, Big Flat Mountain, Doyle River.

*PYLAISIA SELWYNII* Kindb. Limberlost, Hawksbill, Pocosin Shelter to South River, Big Flat Mountain, Big Run.

## RHYTIDIACEAE

*RHYTIDIADELPHUS TRIQUETRUS* (Hedw.) Warnst. Franklin Cliffs.

*RHYTIDIUM RUGOSUM* (Hedw.) Kindb. Franklin Cliffs, Pocosin Shelter to South River.

## HYLOCOMIACEAE

*HYLOCOMIUM BREVIROSTRE* (P. B.) Bry. Eur. Franklin Cliffs, Hawksbill, Pocosin Shelter to South River.

*HYLOCOMIUM SPLENDENS* (Hedw.) Bry. Eur. Franklin Cliffs.

\**HYLOCOMIUM UMBRATUM* (Hedw.) Bry. Eur. Pocosin Shelter to South River.

## DIPHYSCIACEAE

*DIPHYSIUM FOLIOSUM* (Hedw.) Mohr. Little Devils Stairs, Buck Hollow, Pinnacle Ridge, Hawksbill, Rose River, Lewis Mountain, Ivy Creek, Doyle River.

## POLYTRICHACEAE

*ATRICHUM ANGUSTATUM* (Brid.) Bry. Eur. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Limberlost, Old Rag, Hawksbill, Lewis Mountain, Pocosin Fire Road, South River, Ivy Creek, Big Run.

*ATRICHUM ANGUSTATUM* var. *PLURILAMELLATUM* (Jennings) Frye. Jones Run, Doyle River, Big Run.

*ATRICHUM MACMILLANI* (Holz.) Frye. Buck Hollow.

*ATRICHUM UNDULATUM* (Hedw.) Beauv. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Limberlost, Old Rag, Hawksbill, Lewis Mountain, Pocosin Fire Road, Pocosin Shelter to South River, Big Flat Mountain, Ivy Creek, Big Run.

*POGONATUM PENNSILVANICUM* (Hedw.) Paris. Little Devils Stairs, Buck Hollow, Hawksbill, Franklin Cliffs, Pocosin Shelter to South River, Big Flat Mountain, Loft Mountain, Ivy Creek, Doyle River, Big Run.

*POLYTRICHUM COMMUNE* Hedw. Old Rag.

*POLYTRICHUM JUNIPERINUM* Hedw. Little Devils Stairs, Big Flat Mountain.

*POLYTRICHUM OHIOENSE* Ren. & Card. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Old Rag, Hawksbill, Rose River, Lewis Mountain, Pocosin Fire Road, South River, Ivy Creek, Doyle River, Big Run.

\**POLYTRICHUM PILIFERUM* Hedw. Hawksbill.

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## THE TAXONOMY OF THE GENUS *SAUVAGESIA* (OCHNACEAE)

JOHN D. DWYER

From the viewpoint of floral structure perhaps no genus of the tribe Luxemburgieae (Ochnaceae),<sup>1</sup> with the possible exception of *Tyleria* Gleason, is more interesting than the herbaceous or suffrutescent genus of the New World *Sauvagesia* L.<sup>2</sup> Not only is the character of the androecium in particular of morphological significance but it is perhaps the most obvious structural feature linking this genus with many of the other genera of the tribe. It is composed of a whorl of five discrete petaloid segments (interior corona) enclosing a regular whorl of five stamens, the interior corona itself encompassed usually by one or several rows of small polymorphic segments (exterior corona). Three genera of the tribe: *Lavradia* Vell., *Leitgebia* Eichl., and *Tyleria* Gleason have a well-defined interior corona. *Lavradia* has five petaloid segments fused into an urceolate cup; the five much reduced androecial segments of *Leitgebia* are united at the base to form a cup-like structure around the ovary; *Tyleria*, on the other hand, has an interior corona of ten uniseriate segments, five of which are large and petaloid and united basally into a cup and the other five of which are smaller and spatulate or obovoid, alternating individually with the larger segments. In addition to the androecium the close relationship of this quartet is also manifested by their elongate-subulate style borne atop a tricarpellate carnose and subrotund ovary, as well as by the scarious sepals which persist on the mature scarious capsules, the latter bearing non-alate seeds (except in *Tyleria*). The genus *Poecilandra* Tulasne seemingly links the above complex to *Blastemanthus* Planch., and thus to some of the more remote genera of the Luxemburgieae: *Cespedezia* Goudot, *Godoya* R. and P., *Krukoviella* A. C. Smith, and *Rhytidanthera* van Tieghem, all of which are arborescent and characterized by crassate sepals, substylate secund crassate pistils with radially arranged stigmas, and coriaceous capsules with alate seeds. I have discussed the relationship of *Poecilandra* and *Blastemanthus* to this latter complex in a previous paper.<sup>3</sup>

<sup>1</sup> This paper was submitted as part of a thesis on the *American Genera of the Tribe Luxemburgieae* (Ochnaceae), in partial fulfillment of the requirements for the degree of Doctor of Philosophy, Biological Laboratories, Fordham University Graduate School, New York, N. Y.

<sup>2</sup> *Sauvagesia erecta* occurs in Africa, where it has probably been introduced.

<sup>3</sup> Bull. Torrey Club 71: 175-178. 1944.

## TAXONOMIC HISTORY OF THE GENUS SAUVAGESIA

*Sauvagesia*, described originally by Linnaeus (Sp. Pl. 1: 203. 1753), was made the type genus of the Violarieae by Gingins (9) and maintained in the Violaceae by Meissner (12) and Bentham and Hooker (4). Subsequently, St. Hilaire (14) and Martius and Zuccharini (11) placed it in the Frankeniaceae and Droseraceae respectively. Planchon (13) was the first to relate it to the Ochnaceae. Baillon (2), in turn, although placing *Sauvagesia* in the Violaceae as a tribe, related this family to the Ochnaceae. A distinct family Sauvagesiaceae (or *ordo distinctus* Sauvagesieae) was proposed by Bartling (3) and accepted by Grisebach (10), Endlicher (6), Eichler (5), and van Tieghem (15), the first two workers relating the family to the Guttiferae, Frankeniaceae, and Hypericaceae, while Eichler placed the family in the Parietales near the Violaceae. Engler (7) concluded the 19th century history of *Sauvagesia* by uniting it to the Ochnaceae as a subtribe of the Luxemburgieae, the subtribal division being subsequently discarded by Gilg in his recent (8) survey of the Ochnaceae. I concur with Gilg's opinion.

## THE ANDROECIUM OF SAUVAGESIA

As indicated previously the staminodia are especially significant in the Sauvagesias. Heretofore no attention has been directed to a character of the segments of the inner corona which is common to most of the species of the genus and itself of evolutionary importance: the vertical submedian ventral ridge and corresponding dorsal furrow of each segment (also found in all the species of *Leitgebia* and *Tyleria*). With the discovery of *S. deficiens* Smith and *S. smithiana* Dwyer the variability of this character becomes evident. Coupled with the fact that the segments of the inner corona of both of these species, which are endemic to the Pacaraima Mountains on the British Guiana-Venezuela border, are obviously broader than those of the remaining species of the genus is the fact that the median ridge is not present but is replaced by two to several well-spaced and irregular-ascending veins arising from the base of each segment. This in my opinion, represents a primitive condition in the evolutionary trend of the genus.

Studies have shown that the presence or absence of the segments of the exterior corona, numbers of whorls and segments, and fasciculate character of the segments cannot be relied upon as stable and constant specific characters. Not only have I been unable to segregate several species hitherto considered distinct (e.g., *S. fruticosa* Mart. and Zucc. and *S. angustifolia* Ule) from *S. sprengelii* St. Hil. on the basis of vegetative characters, but also on the nature of the outer corona. Both Eichler (5) and Gilg (8) employed the latter as a main character in their keys to species. Numerous dissections, however, have made it clear that the segments of the exterior corona range from being densely fasciculate to being completely suppressed. Since this condi-



tion was often found to occur in different flowers from the same plant, its intraspecific value becomes doubtful. Similar variations of the exterior corona are to be found in the more widely collected species *S. erecta* L. and *S. brownei* Planch.

As for the interior corona, observations, particularly on the staminodia of *S. brownei*, indicate that this whorl probably represents a fusion of segments similar to those of the exterior corona, since this species shows frequently the basal parts of the segments fused into a single petaloid segment with the swollen capitate portions free. Upon dissecting a flower of one specimen (*Archer 1809*, NY), it was found that one segment of the interior corona bore a small lateral anther-like appendage.<sup>4</sup> Another flower from this specimen showed one of the segments of the interior corona bearing a basal and lateral falcate appendage similar to those found at the base of the free inner portions of the corona of *Tyleria floribunda* Gleason.

Despite the instability in the presence, number, and fasciculate character of the staminodia of the outer corona these manifest remarkable constancy in their *morphology* except in *S. brownei*. This species, confined to the West Indies, is obviously related to *S. erecta*, particularly in having the bostryches of flowers extending in most cases, to the middle of the stem. The frequent fusion among staminodial segments of the same whorl of *S. brownei* make it probable that this species is experiencing a transitional period in its evolution. This apparent attempt to effect a complete fusion of the parts of these whorls approaches the condition found in the species of *Lavradia*, *Tyleria*, and *Leitgebia*.

#### GEOGRAPHICAL DISTRIBUTION AND ECONOMIC IMPORTANCE OF SAUVAGESIA

Of the sixteen species of *Sauvagesia* one is pantropical—*S. erecta* L.; one is endemic to the West Indies—*S. brownei* Planch.; three are comparatively well distributed through northern South America and scattered throughout the West Indies—*S. erecta* L., *S. tenella* Lam., and *S. sprengelii* St. Hil. The remaining species are endemic to the Pacaraima Mountains and are localized in distribution.

Apparently the Sauvagesias are of little economic importance. Saint Hilaire (14) and Eichler (5), doubtlessly basing their statements on the notes of previous writers, e.g., Aublet (1), note that the mucilaginous exudate of the weed *S. erecta*, termed by various workers "Ironweed," "Herb of St. Martin," and "Adima" is used as a balm on inflamed portions of the body as well as internally as a purgative.

<sup>4</sup> In my opinion, which is based on observations of abnormal segments of the inner corona, the median ridge of the inner corona is homologous with the filaments of the stamens and the lamina of the segments homologous with the thecae. Similar and more striking instances of the intimate relationship between the stamens and the segments of the interior corona may be found in the closely related family Violaceae.

## SAUVAGESIA L. Sp. Pl. 1: 203. 1753.

*Sauvagea* Neck. Elem. 2: 378. 1790.*Roraimanthus* Gleason, Phytologia 1: 39. 1933.

Herbs; branches smooth, glabrous, the stem rarely simple; roots fibrous; leaf-blades subsessile, entire or glandular-serrate, the teeth minute, often revolute or curled, the costa prominent above and below, the secondary veins sharply ascending and prominent; stipules persistent; the cilia few to many,

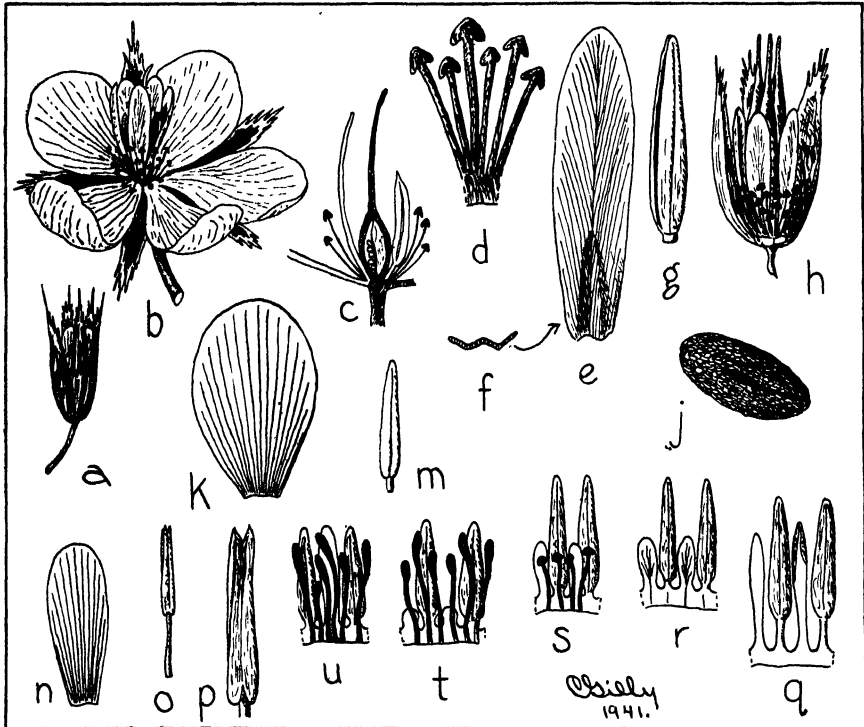


FIG. 1. *Sauvagesia longifolia* Eichl.: a—bud ( $\times 3$ ); b—flower ( $\times 3$ ); c—longitudinal section through flower ( $\times 6$ ); d—portion of outer coronal ring ( $\times 10$ ); e—cross section through the basal portion of inner corona segment, the dorsal face downward; f—stamen, showing longitudinal dehiscence of thecae ( $\times 10$ ); g—capsule, with two of the persistent sepals removed, showing the persistent coronas ( $\times 4$ ); h—seed ( $\times 20$ ). (Drawn from Tate 1314.) *S. smithiana* Dwyer: k—coronal segment ( $\times 10$ ); m—stamen ( $\times 10$ ). (Drawn from Tate 321, TYPE.) *S. tenella* Lam.: n—coronal segment ( $\times 10$ ); o—stamen ( $\times 10$ ); p—anther, showing free apical portion of the thecae ( $\times 20$ ). (Drawn from Allen 830.)

filiform, sharply ascending; flowers 2–6 in bostryches or solitary on a shortened axillary peduncle or solitary on short pedicels, the bostryches fasciculate in the axils of the uppermost leaves or borne on a paniculate rachis or axillary in the stem leaves; sepals 5, quincuncial, expanded at anthesis, appressed and persistent in fruit; petals 5, imbricate in bud, red white or violet, soon

deciduous, usually clawed at base; segments of exterior corona present or absent, numerous or rarely few, in 1-3 continuous whorls or fasciculate and opposite to the stamens, unequal, often heteromorphic and in same whorl as stamens, usually filamentous, clavate, anchor-shaped or reniform at apices, shorter than segments of interior corona, persistent in fruit; segments of interior corona 5, free, petaloid, obovate, elliptic, rotund or rarely subulate, shorter than petals in length, with or without a distinct ventral ridge and dorsal furrow, the veins flabellate and subprominent, persistent in fruit; stamens 5, persistent in fruit, the anthers narrow-oblong (rarely subrotund or ovate), rarely exceeding segments of interior corona in length, obtuse or subcordate at base, 4-celled, dehiscing longitudinally, the filaments short (or rarely exceeding anthers in length); ovaries conic, 3-lobed, the styles subulate, the stigmas indeterminate, the ovules borne on 3 parietal placentae extending up most of wall of ovary; capsules turgid, drying dark-brown, irregular-striate, ovate to ovate-elliptic, equal to or exceeding persistent sepals, acute at apices, the styles eventually deciduous, the seeds plump, oblong, and reticulate (fig. 1).

TYPE SPECIES: *Sauvagesia erecta* L. This plant, a common pantropical weed, is perhaps the best known species of the genus and of the tribe Luxemburgieae.

The author wishes to thank the Directors of the institutions listed below who are kind enough to allow him to examine herbarium material of *Sauvagesia*. For purposes of citation a letter designating the institution is used:

Chicago Museum of Natural History, Chicago, Ill. (F).

New York Botanical Garden, New York, N. Y. (NY).

United States National Herbarium, Washington, D. C. (US).

The author wishes to express especial thanks to Dr. A. C. Smith who assisted him so materially in the preparation of this paper and to Mr. Charles Gilly for his invaluable criticism and excellent drawing.

#### KEY TO SECTIONS

- Exterior corona (when present) heteromorphic; interior corona heteromorphic, the segments alternating (or seemingly so) with the stamens; flowers few in axillary bostryches. 1. *Browneae*.
- Exterior corona (when present) regular; interior corona regular, forming 1-3 distinct whorls outside the stamens; flowers few to numerous, rarely solitary, usually in terminal or axillary bostryches. 2. *Imthurnianae*.
- Flowers solitary on a short bracteolate peduncle. 3. *Longifoliae*.
- Flowers borne in bostryches (in one species simply solitary and axillary). 4. *Smithianae*.
- Anthers oblong, subsessile. 5. *Linearifoliae*.
- Segments of interior corona oblong or obovate, the median longitudinal furrow and ridge distinct.
- Segments of the interior corona subrotund, without a median ridge and furrow.
- Anthers ovoid (in *S. tenella* oblong), the filaments almost equal to or exceeding the anthers in length.

#### KEY TO THE SPECIES

##### 1. *Browneae*

Staminodial segments heteromorphic.

1. *S. brownei*.

2. *Imthurnianae*

Flowers solitary on a short bracteolate peduncle.

2. *S. imthurniana*.

3. *Longifoliae*

Bostryches in the axils of the leaves at least above the middle of the stem.

Leaves oblong-lanceolate, the middle leaves up to 2 cm. long, gradually tapering at the base.

3. *S. erecta*.

Leaves broadly lanceolate, the middle leaves up to 4 cm. long, tapering acutely at the base.

4. *S. grandifolia*.

Bostryches aggregated in a strictly terminal inflorescence.

Inflorescence racemiform; pedicels at least 0.5 mm. wide; sepals 3-6 cm. long, ascending.

Leaves lanceolate, linear-lanceolate or oblong-lanceolate, 0.8-12 cm. long, ascending.

Leaf-blades without prominent secondary veins, the latter arcuate-ascending, joining the costa at a wide angle.

Median leaves 7-12 cm. long, lanceolate, acute at apices; leaf-margins not conspicuously callose; stipules obtuse and non-fimbriate at base.

5. *S. elata*.

Median leaves 2.5-3.5 cm. long, oblong-lanceolate, round-obtuse at apices, the margins distinctly callose-revolute; stipules fimbriate-ciliate at base.

6. *S. racemosa*.

Leaf-blades striate with prominent secondary veins, the latter joining the costa at an acute angle.

Leaves 1.1 cm. or less in length, crowded; apices of sepals ciliate or eciliate.

7. *S. sprengelii*.

Leaves 3-9 cm. long, well-spaced; apices of sepals ciliate (about 2 mm. long).

8. *S. longifolia*.

Leaves ovate, up to 0.7 cm. long, somewhat deflexed.

9. *S. amoena*.

Inflorescence paniculate; pedicels up to 0.2 mm. wide; sepals 2-2.5 mm. long.

10. *S. ramosissima*.

4. *Smithianae*

Sepals unequal, mostly erose-marginate at the apex; veins of segments of interior corona numerous and parallel-ascending.

11. *S. deficiens*.

Sepals equal, acuminate at apex; veins of the segments of interior corona 3+, branching obliquely above the middle.

12. *S. smithiana*.

5. *Linearifoliae*

Leaves linear, stiff, coriaceous; exterior corona present.

Leaf-blades ascending; flowers fasciculate in racemes (anthers elongate, ovoid); sepals with a long terminal cilium subtended by long marginal cilia.

13. *S. linearifolia*.

Leaf-blades deflexed; flowers few, terminal, solitary in the axils of the uppermost leaves; anthers linear-ovate, abruptly apiculate at the apex.

14. *S. deflexifolia*.

Leaves not linear, membranaceous or glandular-fleshy; exterior corona absent.

Stipules not glandular-jointed; anthers oblong; secondary veins of leaves inconspicuous above.

16. *S. tenella*.

Stipules with cilia bearing glandular-joints; anthers subrotund or ovate; secondary veins of leaves inconspicuous above.

15. *S. pulchella*.

## 1. SAUVAGESIA BROWNEI Planch. in Urban Symb. Ant. 5: 430. 1908.

*Sauvagesia stenophylla* Urban, Repert. Sp. Nov. 22: 39. 1925.

*Sauvagesia microphylla* Urban, Repert. Sp. Nov. 22: 39. 1925.

Woody herbs, 5–45 cm. high; branches basal, smooth, elongate or short and densely foliose; petioles up to 2 mm. long; leaf-blades crowded or up to 1 cm. apart, chartaceous, often stiff, the lamina distinctly revolute or plane, elliptic or linear-elliptic, 0.4–1.9 cm. long, at least twice as long as broad, acute at apex, subcuneate at base, the margin callose, the teeth minute and glandular, the secondary veins subprominent above, oblique-ascending; stipules narrow-triangular, the cilia elongate, ascending, arranged in threes at apices of stipules; flowers usually 2 per bostryx, axillary in uppermost leaves, the fascicles (or flowers seemingly solitary) extending to middle of stem, the pedicels shorter than or up to twice length of buds; sepals subequal, lanceolate or elliptic-oblong, 2.5–4.5 mm. long, acute and terminating in a long cilium up to 1.5 mm. long, the veins 5–7; petals obovate-rotund, narrow-obovate or broadly elliptic, 2.5–5 mm. long, equal to or exceeding sepals in length; segments of exterior corona present or absent, numerous to few, in continuous whorls or fascicles, often seemingly in same whorl as stamens, reniform-capitate to subulate, smaller than, equal to or exceeding segments of interior corona in same whorl as stamens and alternate with them, polymorphic (often in same flower), mostly linear, subulate, lanceolate or oblong, up to 1.2 mm. long, acute, obtuse or rostrate at apex; anthers linear, 1.2–1.8 mm. long, the filaments up to 0.8 mm. long, never more than half the length of anthers; ovaries narrowly or widely ovate, 0.7–1.2 mm. long, the styles subulate, 0.8–1.2 mm. long; capsule ovate-oblong, equal to or exceeding sepals in length (fig. 1, *q-u*).

TYPE LOCALITY: Between Mt. Diable and Mt. St. Ann, Jamaica.

DISTRIBUTION: Cuba and Jamaica.

CUBA: Without locality, *Wright 2130* (NY); Pinar Del Rio, Laguna Santa Maria, Britton, Britton, and Earle 7168 (NY); Sierra de Cabra, Britton, Britton, and Gager 7286a (NY); Savanna de Herradura, Britton, Britton, et al. 6467 (NY); San Juan y Martinez, Ekman 18056 (NY, type collection of *S. microphylla*); Herradura, van Hermann 566 (NY); Guane, Leon and Roca 7021 (NY); Arroyo Galiano, O'Donovan 5228 (NY); Luis Lazo, O'Donovan 5296 (NY); Laguna Jovero, Shafer 10748 (NY), 10865 (NY); Guane, Shafer 10507 (NY); Without locality, Shafer and Leon 3412 (NY); Isle of Pines: Nueva Gerona, Curtiss s. no. (NY); Nueva Gerona, Jennings 657 (NY); Santa Clara: La Cunagua, Britton, Britton and Wilson 14551 (NY); Cienfuegos, Combs 435 (NY); Without locality, Leon 6403 (NY); Banao Mts., Naranjo China, Leon and Roca 8079 (NY); Manacas, Leon and Cazanias 5895 (NY); Lomas de Banao, Luna 131 (NY); Oriente: Sierra de Nipe, Ekman 2691 (NY); Arroyo del Medio, Shafer 3640 (NY), Baracoa, Underwood and Earle 1355 (NY). JAMAICA: Without locality, Alexander s. no. (NY); Moody's Gap, Britton 3369 (NY); Dolphin Head, Britton and Hollick 2200 (NY); Caselton Garden, Fawcett 8003 (NY); Bradau Hill Rd., Fawcett 8470 (NY); Upper Clarendon, Harris 12256 (NY); Portland, Mazon and Killip 96 (NY); Prospect Hill, Thompson (F); Bull Head, Underwood 3363 (NY).

*S. brownei*, on the basis of vegetative characters, shows strong affinity with *S. erecta*. Examination and dissection of many flowers of both species have shown, however, that the staminodial segments of the former species are heteromorphic while those of the latter are consistently homomorphic. The isolation of *S. brownei* in the West Indies is also suggestive of the distinctness of the species.

*S. microphylla* and *S. stenophylla*, both described by Urban, lack characters sufficiently strong to warrant giving these species specific rank. They are

probably mere ecological variants which on superficial examination appear to be different from *S. brownei*.

2. *SAUVAGESIA IMTHURNIANA* (Oliver) Dwyer, Bull. Torrey Club **67**: 291. 1940.

*Leitgebia imthurniana* Oliver, Trans. Linn. 2: 271. 1877.

*Roraimanthus imthurnianus* (Oliver) Gleason, Phytologia 1: 39. 1933.

Small shrubs, ericoid in habit, up to 30 cm. high; branches patent and angular-ascending; stem nigrescent and rough with persistent bases of stipules; leaf-blades imbricate at summit of branches, sessile, coriaceous, obovate-oblong or sublanceolate, about 9 mm. long, 2–3.5 mm. wide, obtuse at apex and base, the margins callose, glandulose-serrulate above middle, the costa prominent above and below, the secondary veins striate, ascending at a sharp angle; stipules scale-like, deltoid to deltoid-lanceolate, 1.5–2.7 mm. long, the cilia strongly ascending; flowers large, about 1.8 cm. wide at anthesis, terminal, 1–3, one usually persistent on peduncle, the latter arising from the axils of uppermost leaves, up to 1 cm. long, bearing four whorled alternate bracts, the uppermost fertile, the pedicels 1.5–2.8 mm. long, the lower pair long-ciliate toward apex, ensheathing stem in a three-quarter circle, the upper pair long-ciliate and tripartite; sepals unequal, lanceolate, 5.7–7.5 mm. long, 1.5–1.8 mm. wide, acute and minutely erose-glandular at apex, obtuse at base, the base with distinct dorsal glandular areas, the margins entire or minute-scabrid; petals equal, pink, obovate, about 6.5 mm. long, about 4.7 mm. wide, obtuse at apex and base, rounded at point of articulation, the veins slender, evanescent, scarcely flabellate; segments of interior corona subplane, narrow-rectangular or obovate-rectangular, 3.7–3.9 mm. long, 0.9–1 mm. wide, obtuse-rotund at apex, tapering slightly toward base, the longitudinal ridge distinct, the furrow scarcely distinct; anthers oblong-rectangular, 1.3–1.5 mm. long, apiculate (the apiculum 0.2–0.25 mm. long), the filaments about 0.65 mm. long; ovaries ovate-conical, about 2 mm. long; carpels glandular, smooth, ovate-triangular, shorter than or equal to sepals in length, about 2 mm. wide, the apices of carpels reflexed at anthesis, dehiscent at least to middle, the veins few, subprominent, well spaced, branching laxly.

TYPE LOCALITY: Summit of Mt. Roraima, British Guiana-Venezuela boundary line.

DISTRIBUTION: Known only from the summits of Mt. Roraima and Mt. Auyan-Tepui, British Guiana-Venezuela.

BRITISH GUIANA-VENEZUELA BOUNDARY LINE: Summit of Mt. Roraima, *Pinkus* 116 (NY); *Tate* 400 (NY); Mt. Auyan-Tepui, *Tate* 1130 (NY).

Undoubtedly the strongest specific characters of *S. imthurniana* are to be found in the stipules and inflorescence. I consider the multi-bracted stalks of the flowers to be peduncles, which by the almost complete abortion of the flowers become pedicellary in nature.

3. *SAUVAGESIA ERECTA* L. Sp. Pl. 1: 203. 1753.

*Sauvagesia adima* Aubl. Hist. Pl. Guian. Fr. 1: 251. 1775.

*Sauvagesia peruviana* R. and S. Syst. Veg. 5: 457.

*Sauvagesia nutans* Pers. Syn. Pl. 1: 253. 1805.

*Sauvagesia gemininiflora* Sess. and Moc. ex Ging. in DC Prodr. 1: 315. 1824.

*Sauvagesia rubiginosa* St. Hil. Mém. Mus. 11: 101. 1824.

*Sauvagesia laza* Mart. and Zucc. Nov. Gen. 1: 38. 1824.

Woody herbs or subshrubs, 5–60 cm. tall, simple or branching profusely, often bushy in habit or with elongate lax branches; stem rubescent, rough (when lower leaves deciduous) with remnants of stipules; petioles scarcely measureable or up to 5 mm. long; leaf-blades well-spaced or crowded into loose or dense clusters, papyro-membranaceous, often stiff (especially the very narrow leaves), striate, oblong-lanceolate, 1.2–6 cm. long, at least twice as long as broad, 0.3–1.2 cm. wide, acute at apex, distinctly cuneate at base, the margins callose, distinctly so beneath, the teeth glandular, appressed, falcate, minute, 1–1.5 mm. apart, the costa prominent above and below, the secondary veins distinctly prominent above, evanescent, rarely distinct (if so, plane and blending with lamina), 1–1.5 mm. apart, spreading somewhat arcuately at a 60° angle from costa, the tertiary veins irregular-parallel to secondary veins and somewhat prominent above; stipules striate, linear-subulate, 4.5–5.5 mm. long, the cilia well-spaced, ascending at oblique angle, elongate, the middle ones 3.5–6.5 mm. long; flowers 1–3 per bostryx (often only one mature per bostryx) in axils of middle or apical leaves, the pedicels usually deflexed, slender, up to 2 cm. long, normally 2–3 times length of flower; sepals green-herbaceous, mostly equal, elliptic-lanceolate to subovate, 3.8–6 mm. long, acute at apex, usually with long terminal cilium subtended by shorter marginal cilia, the veins 4–8, prominent, strongly ascending, the margin entire or with red-glandular cilia; petals mostly obovate (or rarely broadly obovate-elliptic), up to 6 mm. long, usually longer than sepals at anthesis, tapering obtusely at apex, broadly or distinctly clawed beneath, the veins well-spaced, subflabellate, branching above middle; segments of exterior corona rarely absent, numerous in 1–3 continuous whorls, round to reniform-capitate, the filaments slender or somewhat expanded, 1–2 mm. long, up to one-half length of interior corona, the innermost the longest; segments of interior corona petaloid, free to base, oblong-obovate (rarely linear-obovate), 3–5 mm. long, rotund or truncate at apex, tapering toward base, the median prominence conspicuous and expanded at base, becoming ridge-like above, the veins oblique and mostly prominent; anthers oblong or linear-oblong, usually 2–2.5 mm. long (rarely up to 3.5 mm.), up to four-fifths length of interior corona, apiculate or vaguely retuse at apex, elongate-ovate or subrotund, 0.8–1.5 mm. long, tapering acutely or obtusely toward base of style, usually smooth, the three lobes conspicuous, the style subulate, 1.6–3.5 mm. long; capsule barely exceeding or distinctly exceeding sepals in length, 3.5–7 cm. long.

TYPE LOCALITY: Dominica, West Indies.

ILLUSTRATIONS: Aubl. Hist. Pl. Guian. 3: pl. 100, as *S. adima*, 1775. Jacq. Sel. Stirp. Am. Hist. Pict. pl. 77. 1780. St. Hil. Mém. Mus. Hist. Nat. Paris 11: 115, pl. 6, as *S. rubiginosa*, 1824. E. and P. Nat. Pfl. 3. 6: 150. 1893.

DISTRIBUTION: Widely distributed through tropical America and the West Indies. Reported by numerous authors to be pantropical.

MEXICO<sup>5</sup>: Chinantla; Galeotti 7177 (NY). GUATEMALA: Los Amates, Bartlett 126 (NY). BRITISH HONDURAS: Yucatan Pen., Gentle 1007 (NY). PORTO RICO: Britton

<sup>5</sup> As the collections of *S. erecta* have been so numerous, I have omitted the greater part of them.

and Cowell 4079 (NY). HAITI: Dept. du Nord: Plaisance, *Leonard* 9320 (NY). SANTO DOMINGO: Barrero, *Eggers* 2044 (NY). GUADELOUPE: Camp Jacob, *Duss* 2439 (NY). DOMINICA: Mantipo River, *Hodge* 478 (NY). MARTINIQUE: Without locality: *Egler* 294 (NY). ST. KITTS: Without locality, *Britton* and *Cowell* 297 (NY). TRINIDAD: South of Dabadie, *Britton* and *Britton* 2469 (NY). PANAMA: Bocas del Toro, Bocas Island, *Cooper* 465 (F). FRENCH GUIANA: Cayenne; *Broadway* 192, 535 (NY); *Leprieur* s. no. (NY). DUTCH GUIANA: Paramaribo, *Samuels* 14 (NY). BRITISH GUIANA: Demarara River, *Anderson* 153 (NY); Upper Mazuruni River, *De la Cruz* 2071, 2084, 2187 (NY). VENEZUELA: Bolivar: Ciudad Bolivar, *L. H. Bailey* and *E. Z. Bailey* 1663 (NY). COLOMBIA: Notre de Santander: Mesa de los Santos, 1400 m. alt., *Killip* and *A. C. Smith* 20839 (NY); Huila: Neiva, *Rusby* and *Pennell* 1062 (NY); Tolima: San Lorenzo, 800 m. alt., *Pennell* 3535 (NY); El Cauca: Puerto de Bueneventura, *Triana* s. no. (NY), 2866 (†) (NY). PERU: Amazonas: Mouth of Rio Santiago, *Tessmann* 4103 (NY); San Martin: Zepelacio, 1600 m. alt., *Klug* 3404 (NY); Loreto: Pongo de Manseriche, *Killip* and *A. C. Smith* 29134 (NY); Iquitos, *Tessmann* 3647 (NY). BOLIVIA: Beni: Rurrenabaque, *Cardenas* 1896 (NY); La Paz: Tipuani, 1400 m. alt., *Buchtien* 5450 (NY); Santa Cruz: Yapacani River, *Kuntze* s. no. (NY). BRAZIL: Without locality, *Riedel* s. no. (NY); Amazonas: Rio Negro and Taquera, *Holt* and *Blake* 563 (NY); Maranhão: *Snethlage* 87 (F); Pernambuco: *Gardner* 920 (NY); Bahia: Without locality, *Glocker* 27 (NY); Matto Grosso: *Kuntze* s. no. (NY); Minas Geraes: Without locality, *Claussen* 296 (NY); Rio de Janeiro: Without locality, *Martins* 296 (NY); São Paulo: Without locality, *St. Hilaire* 998 (†) (NY).

Common Names: "Herb of St. Martin," "Ironweed," and "Adima."

*S. erecta*, the type species of the genus, has the broadest geographical range of any American or West Indian species of the Ochnaceae. Its center of distribution appears to be in the West Indies, although I have not seen material from Cuba, apparently being replaced in this region by *S. brownei*. The leaves of the West Indian collections of *S. erecta* are usually large, the fascicles or bostryches are well spaced along at least the upper half of the stem, and the flowers are usually borne on elongate pedicels. Narrower leaf types with shorter pedicels and somewhat compressed bostryches are common throughout the Andean range of the species.

Although *S. erecta* shows definite relationships with *S. brownei*, particularly in the spacing of the bostryches along the stem, I have separated the former from the latter because of the differences in the structure of the staminodia of the two species.

4. *Sauvagesia grandifolia* Dwyer, sp. nov. Herba lignosa; petiolo 3-5 mm. longo; laminis foliorum chartaceis late ellipticis, 3.5-6 cm. longis, 1.0-1.9 cm. latis, apice acutis basi angusto-attenuatis margine serrato praeter base dentibus 1-3 mm. distantibus, costa utrimque subplana venibus principalibus secundariis 12-14 ascendentibus supra subprominentibus subter subplanis, 1-2.2 mm. distantibus, venis tertiariis subparallelis arcuato-ascendentibus ad marginem in laxo reticulo dispositis; stipulis lineare-subulatis, 1-1.5 cm. longis, ciliis elongatis distantibus ramulosis basi margine gracile scariosoque; floribus 2-3 per bostrychem axillarem secundum longitudinem caulis dispositam pedicellibus 2 ± cm. longis; gemmis lineare-ovatis, 1 cm. longis, 3.1-3.5 mm. latis; sepalis aequalibus, lineare-lanceolatis aut lanceolatis, circ. 9 mm. longis, 2.7 mm. latis, basi obtusa apice acuminata margine



integro aut ciliis ascendentibus glandularibus apice cilio ad 9 mm. longo; petalis ellipticis apice triangularibus venis flabellatis; coronae exterioris segmentis multis 2-3 seriatis filamentosis reniforme-capitatis vel rotundo-capitatis, 0.8-1.5 mm. longis segmentis coronae interioris oblongo-rectangularibus vel angusto-obovatis, 4.5-8 mm. longis, 1-1.7 mm. latis, apice truncatis erosisque medio jugo distincto venis flabellatis, antheris lineare-rectangularibus, 3-5 mm. longis, apice basique obtusis, filamentis teretibus, ad 0.5 mm. longis, ad 1.2 mm. latis, stylis triangularibus, ad 3 mm. longis, ad 1.2 mm. latis, stylis linearibus, ad 2.6 mm. longis; fructibus non visis.

TYPE LOCALITY: Petropolis, Rio de Janeiro, Brazil.

DISTRIBUTION: Known only from the type locality.

BRAZIL: Petropolis, Rio de Janeiro, *Glaziou 6478* (US, TYPE COLLECTION).

This species is obviously related to *S. erecta*, principally in the arrangement of the bostryches which are disposed along the length of the stem. Its very large chartaceous and elliptic leaves readily distinguish it from its ally.

5. *SAUVAGESIA ELATA* Benth, London Jour. Bot. 4: 107. 1842. Low shrubs up to 1 m. high, the stem thick, glandular, striate, usually somewhat prostrate at base; roots fibrous; petioles of leaves 3-5 mm. long; leaf-blades chartaceous, lanceolate, the middle ones usually 6-12 cm. long, 1.5-2.5 cm. wide, acuminate at apex, the margin not callose, the teeth minute, 2-4.5 mm. apart, the costa slender and prominent, indistinct above, the secondary veins slender, arcuate- and lax-ascending, scarcely prominent beneath, the reticulate areas distinct or indistinct; stipules appressed, elongate-deltoid, 1-1.5 cm. long, striate, the marginal cilia elongate, with or without smaller cilia at base; flowers 3-6 per bostryx, crowded in fascicles, the rachis slender 6-10 cm. above the uppermost leaves, mostly simple or bearing angular branches at base, the latter up to 6 cm. long, the pedicels 3.5-6.5 mm. long, the articulation-stalks 1.5-2 mm. long; sepals equal, lanceolate to ovate-lanceolate, about 6 mm. long, acute at apex, the apex terminating in a glandular cilium and rarely bearing glandular teeth; petals white, oblong, as long as or shorter than sepals, entire at apex, retuse, the notch bearing 1-3 glandular cilia, tapering little toward base, the veins numerous and pluriramose; segments of exterior corona numerous in 2-3 continuous whorls, the innermost whorl up to two-fifths the length of the interior corona, filamentous, the apices scarcely swollen; segments of interior corona obovate or oblong, up to 4 mm. long, the median ridge distinct, the veins prominent, well spaced and flabellate from ridge, the apex minutely retuse; stamens oblong or almost subulate, two-fifths the length of interior corona, the filaments short; ovary flask-shaped or simply ovate, the style short and crassate, tapering toward base, a little longer than ovary, the placentae extending up one-half the wall of ovary; capsule ovate-rotund, equal to sepals or rarely up to 4 mm. beyond apex of carpels, the latter scarcely rupturing to middle.

TYPE LOCALITY: British Guiana.

DISTRIBUTION: Known only from British Guiana.

BRITISH GUIANA: Waru-Waru Creek, Pomeroon River, *Barlett 8142* (NY); Amakura, *De La Cruz 3472* (NY); Upper Mazaruni River, *De La Cruz 2286, 2288* (NY); Pomeroon River, *De La Cruz 2988* (NY), *2992* (NY), *3180* (NY); Kaieteur Falls, Potaro River, *De La Cruz 4456* (NY); Yarikita River, *Hitchcock 17652* (NY); Pomeroon District, in *Thurn 1941* (NY); Makauria River, *Sandwith 1569* (NY).

This species has the largest leaf-blades of the *Sauvagesias*; the lamina has distinctly arcuate-ascending veins, a character not present or not as obvious in the other species of the genus.

6. *SAUVAGESIA RACEMOSA* St. Hil. Mém. Mus. Hist. Nat. Paris 11: 98. 1824. Woody herbs, 20–45 cm. high, simple or branching mostly at base, the branches canaliculate; petioles of leaves usually absent, rarely up to 3 mm. long; leaf-blades coriaceous, ascending, 0.5–1.5 cm. apart, oblong-lanceolate, up to 4 cm. long (2.5–3.5 cm. long in middle of stem), obtuse at apex, tapering obtusely or cuneately at base, the secondary veins numerous, 0.5–1.3 mm. apart, arcuate- and parallel-ascending, mostly subplane, the margin distinctly subcallose (especially beneath), the outermost dentiferous part narrow-ate (0.1 mm. wide), the teeth closely appressed and minute; stipules submembranaceous, striate, oblong-deltoid, up to 1.8 cm. long, the cilia elongate with small intermediate cilia along the scarious margin, the corpus basally and eccentrically fimbriate; flowers 1–5 in racemiform fascicular bostryches from the axils of reduced leaves, the fascicles 4–12 mm. apart, the rachis often branched at apex, 4–10 cm. above the uppermost leaves; flowers large, up to 13 mm. wide at anthesis; sepals ovate or oblong, about 5.5 mm. long, obtuse at base, the margins scarious, mostly entire, the veins  $\pm 7$ , ascending and uniting acutely at apex; petals pink, obovate, 7–8.5 mm. long, subacuminate at apex, clawed or merely obtuse at base, the veins well spaced, flabellate, branching near margin; segments of exterior corona in a uniseriate or biseriate ring, the longest segments at least half the length of inner segments, subclavate at apex; segments of interior corona oblong, about same length as sepals, rotund at apex; anthers subsessile, oblong, 2.8–3.5 mm. long, obtuse at apex; ovary about 2 mm. long, the style subulate, up to 5 mm. long, more than twice the length of ovary, somewhat constricted at base; capsules turgid, ovate-triangular, 7–8.5 mm. long, about 4.5 mm. wide, exceeding sepals and segments of interior corona in length, the veins scarcely visible, the carpels purple-black when dry, the style rarely deciduous before dehiscence.

TYPE LOCALITY: Minas Geraës or São Paulo, Brazil.

ILLUSTRATION: St. Hil. Pl. Brés. 1: pl. 1, f. 1, 5. 1824.

DISTRIBUTION: Apparently well distributed throughout Brazil, especially in the southern States.

BRAZIL: *Martius 1304* (NY); *Riedel s. no.* (NY); *Saint Hilaire 1188* (F, frag. of type (!) of *S. racemosa*); *Warming s. no.* (F, NY); Goyas: *Gardner 3009* (NY); Matto Grosso: Cuyabá, *G. D. Smith 332* (NY); Minas Geraës: Pirapora, *Burret, Brady and Mello 10153* (F); São Paulo: *Guilherme 173* (F); Ityrapina, *Guilherme 8329* (NY); Butantan, *Hoehne 784* (F). PARAGUAY: Without locality, *Jorgensen 4721* (F, NY).

## 7. *SAUVAGESIA SPRENGELII* St. Hil. in Bull. Soc. Philom. 2: 173. 1823.

*Sauvagesia erecta* Aubl. Hist. Pl. Guian. Fr. 1: 254. 1775. Not L.

*Sauvagesia erecta* Spreng. Neue. Entdeck. 1: 296. 1820. Not L.

*Sauvagesia serpyllifolia* Mart. and Zucc. Nov. Gen. 1: 37. 1824.

*Sauvagesia fruticosa* Mart. and Zucc. Nov. Gen. 1: 38. 1824.

*Sauvagesia kappleri* Miq. Stirp. Surin. 7: 105. 1851.

*Sauvagesia rosacea* Ule, Notizbl. Bot. Gart. Berlin 6: 344. 1915.

*Sauvagesia angustifolia* Ule, Notizbl. Bot. Gart. Berlin 6: 342. 1915.

*Sauvagesia duckei* Sleumer, Repert. Sp. Nov. 42: 263. 1937.

*Sauvagesia striata* Gleason and Dwyer, Brittonia 3: 169. 1939.

Woody herbs, up to 45 cm. high, ericoid in habit, the basal branches elongate, sharply ascending, the terminal branches somewhat angular and shorter; petioles of leaves up to 1 mm. long; leaf-blades coriaceous, striate, usually persisting at apices of branchlets, smaller leaves often aggregated in axils of larger leaves, the latter about 5.5 mm. apart, lanceolate to linear-lanceolate, up to 1.7 cm. long, rarely up to 2.5 cm. long, up to 0.6 cm. wide, acute at apex, obtuse at base, the margins subcallose and serrate, the costa prominent above and below, the secondary veins 6-7 per side, prominent above, oblique- or strongly ascending; stipules linear or linear-ovate, up to 7 mm. long, the cilia few, ascending, conspicuously 3-ciliate at apex; flowers 2-6 per bostryx, the rachis 2.5-6 cm. long, the bostryches well spaced, the pedicels slender, articulate, up 0.9 cm. long; sepals subequal or distinctly unequal, subpellucid, the outermost smaller, the inner lanceolate, up to 4.5 mm. long, obtuse to acute, eciliate or with a distinct terminal cilium, or the marginal cilia crowded near apex, obtuse at base, often with glandular areas (on outer surface) above the articulation-joint, the margins thin-scarious or scarcely differentiated, the cilia ascending, red-glandular, subulate, the veins  $3-\pm 7$ , branching obliquely and uniting acutely at apex, slender, flabellate; petals white to red, obovate to subcuneate, longer than sepals, obtuse to subcuneate at apex; segments of exterior corona usually numerous, in 2-3 continuous whorls or disposed as discrete fascicles, rarely few or completely absent, filamentous below, expanding into a reniform capitate or clavate apex, up to one-half length of interior corona; segments of interior corona oblong, 3-5 mm. long, 1.2-1.7 mm. wide, distinctly obtuse at apex, the vertical ridge distinct or subplane and tapering up to middle; anthers oblong, 1.3-2 mm. long, obtuse at apex, the filaments distinct, about 0.4 mm. long; ovary ovate or flask-shaped, 0.8-1.2 mm. long, the style subulate, at least twice length of ovary, constricted at base, often geniculate near apex; capsule linear-ovate, extending 2-2.5 mm. above largest sepals.

TYPE LOCALITY: British Guiana.

ILLUSTRATIONS: Mart. and Zucc. Nov. Gen. 1: pl. 25, f. 1-9, 1824. Velen. Vergl. Morphl. Pfl. pl. 7 (fl. of *S. rosacea*), f. 1-3, 1910.

DISTRIBUTION: Known from Trinidad and apparently well distributed through tropical South America.

TRINIDAD: Aripo Savanna, Britton and Britton 2926 (NY); Piarco Savanna, Britton, Britton, and Hazen 61 (NY); Aripo Savanna, Kuntze 1029 (NY). COLOMBIA: Rio Guatiquia, Pennell 1638 (F, NY). PERU: Loreto: Tarapoto: Spruce 4244 (NY); Ule 6352 (F, photo of type of *S. rosacea*). FRENCH GUIANA: Without locality, Leprieu 287 (F); Cayenne: Leprieu s. no. (F, NY); Leprieu 231 (NY). DUTCH GUIANA: Forest of Zandery, Samuels 264, 303 (NY). BRITISH GUIANA: Without locality, Schomburgk 162 (NY); Ituni, Waruni Savanna, Abrahams 45 (NY); Kaieteur Savanna, Hollister s. no. (NY); Essiquibo River, Kurupukari Savanna, A. C. Smith 2172 (NY); Freschal (Mt. Roraima), Tate 23 (NY). VENEZUELA: Kata, Ule 8652 (F, photo and twig of type of *S. angustifolia*); Amazonas: Mt. Auyan-Tepui, Tate 1312 (NY, type of *S. striata*). BRAZIL: Para: Vigia, Drouet 2119 (F); Minas Geraes: Minas Gervis, Ilhoes, Blanchet 1875 (F, NY, type collections of *S. serpyllifolia*).

This species exhibits much diversity in habit, thus accounting for its relatively large number of synonyms. It is well established in the sandy sa-

vannas, having a wide distribution through the eastern sections of north and central South America. The exterior corona, although rather uniform in shape, is frequently fasciculate or entirely absent. This condition suggests that the presence or absence of the segments of the exterior corona is not too reliable a character in the segregation of the species of *Sauvagesia*. *Spruce 4244* (NY) is noteworthy as its flowers invariably show the exterior corona reduced to a few segments. Although Sleumer's species, *S. duckei*, as ascertained from his description, has very large leaves, it cannot be segregated from *S. sprengelii* on the basis of the other characters enumerated.

8. *SAUVAGESIA LONGIFOLIA* Eichl. in Mart. Fl. Bras. **13**(1): 407. 1871. Woody herbs up to 70 cm. high; branches often basal, strongly ascending; leaf-blades subsessile, thin-coriaceous, strongly ascending, 0.8–1.3 cm. apart, linear-lanceolate, 3–9 cm. long, 0.5–0.9 cm. wide, distinctly acute at apex, narrow-attenuate at base, the margin serrate, the teeth minute, glandular, uncinat, the costa prominent above and below, the secondary veins numerous, prominent above, subplane beneath, irregular-ascending, spreading from costa at about 70° angle; stipules appressed, striate, linear, up to 1.5 cm. long, the cilia ascending, as long as or longer than corpus in length; flowers 1–3 in fascicular racemiform bostryches, the latter arising from the axils of reduced leaves, the rachis slender and terminal, up to 10 cm. above uppermost leaves, the fascicles 1–1.3 cm. apart; sepals subequal, striate, lanceolate to elliptic,  $\pm 6$  mm. long, acute at apex, terminating in a long glandular cilium about 2 mm. long, the margins entire or with small ascending, often uncinat teeth, the apical cilia of two sizes; petals obovate, up to 6 mm. long, subclawed at base, obtuse to subacute at apex, the veins flabellate; segments of exterior corona numerous, in 2–3 continuous whorls, reniform-capitate, up to 1.7 mm. long, about one-third length of interior corona; segments of interior corona oblong, up to 4.2 mm. long, obtuse or slightly retuse at apex, the median ridge distinct; anthers subsessile, up to 2.5 mm. long, about or a little more than one-half the length of segments of interior corona, obtuse at apex; ovary ovoid to conic-ovoid, 1–1.5 mm. long, the style awl-shaped, almost 3 times the length of ovary, constricted at base; capsule minutely granular, ovate-rotund, 5.5 mm. long, 3 mm. wide at base, tapering narrowly at apex, scarcely exceeding reflexed tips of persistent sepals (fig. 1, a–j).

TYPE LOCALITY: Cataract Caldnac, Brazil.

ILLUSTRATION: Eichl. in Mart. Fl. Bras. **13**(1): pl. 83. 1871.

DISTRIBUTION: Known from the Pacaraima Mts. on the British Guiana-Venezuela boundary, from French Guiana, and from Brazil.

BRITISH GUIANA—VENEZUELA BOUNDARY: Mt. Auyan-Tepui, 1100 m. alt., *Tate 1314* (NY). FRENCH GUIANA: Without locality, *Leprieu* s. no. (NY). BRAZIL: Without locality, *Sellow* s. no. (F, photo).

9. *SAUVAGESIA AMOENA* Ule, Notizbl. Bot. Gart. Berlin **6**: 341. 1915. Erect herbs up to 40 cm. high, branching at base; leaf-blades rigid, deflexed, subsessile, coriaceous, lustrous-green above, straw-colored beneath when dry, persisting along most of stem, crowded, ovate,  $\pm 7$  mm. long, 4 mm. wide, acute at apex, the costa conspicuous above and below, the secondary veins  $\pm 10$ , arcuate-ascending, more conspicuous beneath, the tertiary veins con-

spicuous beneath, the margins callose with 6 minute ascending teeth; stipules linear-subulate, up to 5 mm. long, the margins subcallose with 5–7 divergent cilia as long as corpus; inflorescence terminal, paniculoid, the branches arising from most terminal leaves; flowers large, about 1 cm. wide at anthesis, 2–3 per bostryx, the fascicles 0.7–1 cm. long, the articulation-stalk 2 mm. long, the outermost bracts leaf-like, up to 3.7 mm. long, tapering toward apex; sepals unequal, ovate to ovate-lanceolate, 3–6 mm. long, erose at apex, bearing a semicircle of minute cilia on apical margin, the base on outer surface often with a yellow glandular area above articulation-joint, the margins scarious, entire or with ascending glandular cilia above middle; petals deep purple, subequal, inversely triangular, 6–8 mm. long, about 5 mm. wide, subrotund at apex, clawed at base, the veins flabellate; segments of exterior corona unequal, numerous, 3-seriate, reniform-capitate or anchor-shaped, 1.1–1.6 mm. long, up to one-fourth length of inner corona; segments of inner corona obovate-elongate, about 4.5 mm. long, united indistinctly at base into a cup, the median ridge of each segment prominent, broad below middle, becoming narrow toward apex, the veins prominent and ascending from ridge; stamens linear-elliptic, 1.5–3 mm. long, obtuse above, the filaments 0.2 mm. long, obtuse above; ovary ovate-rotund, the style about three times length of ovary; capsule narrow-ovate-lanceolate, equal to or exceeding sepals in length, acute at apex.

TYPE LOCALITY: Summit of Katá, Pacaraima Mts., British Guiana-Venezuela boundary.

DISTRIBUTION: Endemic to the Pacaraima Mts., British Guiana-Venezuela.

BRITISH GUIANA—VENEZUELA BOUNDARY: Mt. Auyan-Tepui, *Tate 1313* (NY); Summit of Katá, *Ule 8650* (F, photo of type of *S. amoena*).

*S. amoena* is a rare endemic species marked by its distinctly ovate and often deflexed leaves.

10. *SAUVAGESIA RAMOSISSIMA* Spruce ex Eichl. in Mart. Fl. Bras. **13**(1): 409. 1871. Slender woody herbs up to 30 cm. high; branches rubescent, angular, and patent at apex; leaf-blades sessile, chartaceous, elliptic-lanceolate, up to 1.5 cm. long, 0.3–0.4 cm. wide, 0.5–0.8 mm. apart in middle of stem, acute at apex, cuneate at base, the secondary veins prominulous above, slender and not prominent beneath, the margin with small glandular teeth, distinctly narrow-callose beneath; stipules appressed, striate, linear, 3–5 mm. long, filamentous-ciliate; inflorescence paniculate, the rachis up to 8 cm. long, jointed or zig-zag, the flowers 3–6 per bostryx, the fascicles 0.7–1 cm. apart, distinctly pedunculate, the peduncles angular, slender, patent, ascending, 0.5–2 cm. long, becoming reduced in size toward apex of inflorescence, the pedicels capillaceous, 0.2 mm. wide, 2.5–10 mm. long, the articulation-stalks 0.7–4 mm. long, the bracts pectinose-ciliate, elliptic, up to 3 mm. long, fused with stipule at basal margin; flowers  $\pm$  2 mm. long at anthesis; sepals lanceolate, about 2 mm. long, acute at apex, terminating in a long glandular cilium; petals elongate-obovate, the same length as sepals, retuse at apex, the veins parallel-ascending; segments of exterior corona 1 to numerous, when numerous fasciculate, clavate, or only swollen at apex, up to one-third length of inner corona; segments of interior corona oblong, 1.5 mm. long, emarginate at apex, the ridge thin and median, the dorsal furrow

distinct, the veins flabellate and prominent; anthers oblong-lanceolate, about 0.7 mm. long, tapering acutely at apex, the filaments 0.3 mm. long; ovary ovate-oblong, as long as the awl-shaped style, the ovules few, glandular-verrucose, obovate; capsule ovate-conical, up to 4.5 mm. long, about twice length of sepals, obtuse at apex, the seeds reticulate, obovate, about 0.5 mm. long.

TYPE LOCALITY: Ribenirão, Matto Grosso, Brazil.

ILLUSTRATION: Eichl. in Mart. Fl. Bras. **13**(1): pl. 82. 1871.

DISTRIBUTION: Known only from the type locality, and from a Brazilian collection sans locality.

BRAZIL: Without locality, *Riedel* s. no. (NY).

This rare species is readily distinguished by its patent and paniculate inflorescence. Its peduncles and pedicels are more slender than those of any other woody species of the genus. According to Eichler the plant grows in a very moist habitat.

11. *SAUVAGESIA DEFICIENS* A. C. Smith, *Lloydia* **2**: 194. 1939. Shrubs about 30 cm. high; upper branches striate, the nodes below somewhat rough with remnants of stipules; roots fibrous; petioles of leaf-blades 1–2 mm. long, the leaf blades papyro-membranaceous, elliptic, 9–22 mm. long, 4–7 mm. wide, subcuneate at base, the margin callose, recurved, serrate, the costa subprominent above, prominent beneath, the secondary veins 6–8 on each side ascending; bostryches crowded at apices of branches, 2–4-flowered, arising from axils of uppermost leaf-blades, the pedicels slender, 3–6 mm. long; stipules lanceolate, 2–3 mm. long, the cilia elongate; sepals unequal, lanceolate, oblong-lanceolate, or rarely ovate, 2.7–5 mm. long, acute or somewhat obtuse at apices, the margin entire, glandular-erose at apex; petals white, obovate-rotund, 3–3.5 mm. long, the veins well spaced and flabellate; segments of exterior corona absent; segments of interior corona obovate-rotund,  $\pm$  3 mm. long, the margin entire or trilobed above, the veins serrate, arising from median part of swollen base of each segment; anthers oblong, 2 mm. long, subcordate at base, the filaments distinct; ovary ovate, 1.1–1.3 mm. long, distinctly 3-lobed, the style subulate, a little longer than ovary, somewhat crassate at base; fruit ovate, conical, up to 5.5 mm. long, the carpels almost twice length of sepals, acute, the median veins distinct.

TYPE LOCALITY: Mt. Iramaikpang, Kanuku Mts., British Guiana.

DISTRIBUTION: Known only from the type locality.

BRITISH GUIANA: Mt. Iramaikpang, 975 m. alt., Kanuku Mts., *A. C. Smith* 3640 (NY, type of *S. deficiens*).

12. *Sauvagesia smithiana* Dwyer, sp. nov. Herba lignosa ad 30 cm. alta, ramulis multis valide ascendentibus caule glabra petiolis ad 4 mm. longis laminis chartaceis supra pallide viridis supra mediam caulem persistentibus, 6–12 mm. distantibus, lanceolatis, 1–2.7 cm. longis, 6.5–9 mm. latis, apice acutis costa utimque prominente ad basim expandente nervis secundariis 7–10 utrimque prominentibus subtus colore distinctis, margine utroque dentibus 6–10 uncinatis utroque cum minorem dentem sinu ferente, stipulis ad basim persistentibus linearibus, ad 8 mm. longis, apice constrictis ciliis elongatis apice 3-ciliatis, inflorescentia racemiforme rhachidibus ad 8 cm.

longis, bostrychibus in axillaribus minutorum foliorum pedicellis gracilibus, 4–6.5 mm. longis, articulo saepe a basi pedicelli ad 2.5 mm. longis, floribus sub anthesi circiter 7 mm. latis, sepalis aequalibus lanceolatis vel oblongo-lanceolatis, circiter 4 mm. longis, apice acutis margine integro vel dentibus parvis ascendentibus venis lateralibus  $\pm 7$  conspicuis prominentibusque, petalis brevioribus sepalis obovato-rotundis, 3–3.5 mm. longis, venis distantibus gracilibus vix flabellatisque, segmentis coronae exterioris desinentibus, segmentis coronae interioris pellucidis rotundis vel subrotundisque, 2.5 mm. longis, venis planis  $\pm 3$  oblique a basi ortis ad apicem vix flabellatis ramosisque, antheris oblongis segmentis interioris coronae brevioribus utroque anthero segmenti margine incluso, circiter 1.6 mm. longis, obtusis apice saepe retusis, filamentis 0.3–0.5 mm. longis, ovariis ovatis circiter 1 mm. longis stylis subulatis, 1.8 mm. longis, ovulis paucis ascendentibus, capsulis ovato-conicis, ad 6.5 mm. longis, 1–1.8 mm. super sepalis extendentibus (fig. 1, *k, m*).

TYPE LOCALITY: Mt. Roraima, British Guiana-Venezuela boundary line.

DISTRIBUTION: Known only from the type locality.

BRITISH GUIANA—VENEZUELA BOUNDARY: Mt. Roraima, 1500 m. alt., *Tate 321* (NY, type of *S. smithiana*).

The author has named this species in honor of Dr. A. C. Smith who assisted him so materially in the preparation of this paper.

*S. smithiana* and *S. deficiens*, two endemic species are closely related; the subrotund segments of their inner coronas are unlike those of any other species of *Sauvagesia*. The two species differ in the shape, size, and length of their stipules, in the morphology and venation of the segments of the inner corona, and in the relative size of their sepals. Unlike those of *S. smithiana* the leaf margins of *S. deficiens* are distinctly recurved.

13. SAUVAGESIA LINEARIFOLIA St. Hil. Mém. Mus. Hist. Nat. Paris **11**: 106. 1824.

*Sauvagesia pusilla* Mart. and Zucc. Nov. Gen. **1**: 35. 1824.

Woody herbs up to 15 cm. high; branches of stem few to many, nodes swollen; leaf-blades persistent above, plane, subcoriaceous, 1.5–2.5 mm. apart, ascending, linear, up to 11 mm. long, 0.5 mm. wide, acute at apex, obtuse at base, the margin callose, the teeth well spaced and acuminate, the costa prominent above and below, the secondary veins inconspicuous; stipules linear, longer than nodes, the cilia strongly ascending and in a whorl of 3 at apex; sepals equal, lanceolate, about 1 mm. long, the margin entire or with ascending, appressed, and glandular cilia, the apex terminating in a stout cilium subtended by elongate marginal cilia, the veins 5–7 and prominent; petals elliptic-rotund to obdeltoid, 3–4.6 mm. long, acute at base, the veins flabellate and slender; segments of exterior corona 5–10, 1–2 alternate with each segment of inner corona and up to one-half length of latter; segments of interior corona elliptic, 1.8–2.3 mm. long, the median vein distinct and not conspicuously ridge-like; anthers narrow-ovate, about same length as segments of interior corona, subrostrate at apex, the filaments almost as long as anthers; ovaries subrotund, up to 2.5 mm. long, the styles crassate, a little

longer than ovary, somewhat constricted at base; capsule exceeding sepals in length, the seeds oblong-rotund, about 1 mm. long.

TYPE LOCALITY: Servico do Rio Pardo, Minas Geraës, Brazil.

ILLUSTRATION: St. Hil. Mém. Mus. Hist. Nat. Paris 11: *pl. 2, f. 1-8*, 1824.

DISTRIBUTION: Known from Venezuela and Brazil.

VENEZUELA: Amazonas: Rio Guainia and Rio Negro at mouth of Rio Casiquiari, *Spruce 3513* (NY). BRAZIL: Without locality, *Riedel s. no.* (NY); Goyas: *Gardner 3007* (F. NY); Minas Geraës: Servico do Rio Pardo, 1000 m. alt., *St. Hilaire* (F, photo of type of *S. linearifolia*).

14. *SAUVAGESIA DEFLEXIFOLIA* Gardn. Hook. Ic. 5(1): *pl. 484*. 1842. Woody herbs, erect and slender, up to 70 cm. high; roots fibrous; branches of stem apical, angular, 1-2 mm. wide at base; leaf-blades sessile, deflexed, the proximal part of lamina appressed to stem, coriaceous, narrowly linear-elliptic or ovate-elliptic,  $\pm$  8 mm. long, about 1.3 mm. wide, strongly acuminate and terminating in a stiff cilium or simply with a small obtuse gland at apex, obtuse at base, the secondary veins scarcely visible above, strongly ascending, the tertiary veins slender and parallel, the margins callose, the teeth well spaced, falcate, about 0.5 mm. long; stipules appressed, subulate, 1.3-2 mm. long, the cilia slender, oblique-ascending; flowers 2-5, terminal, not in bostryches but solitary in axils of somewhat reduced apical leaves, about 6 mm. long at anthesis, the pedicels slender, up to 4 mm. long, often obscured by leaf-blades, the flowers seemingly sessile; sepals lanceolate, rarely broadly ovate, up to 4.7 mm. long, subclawed at base, obtuse above, the veins flabellate-ascending; petals white, obovate, about 4.5 mm. long, 3.5 mm. wide, the margins entire below, minutely toothed at apex, the median teeth more distinct; segments of exterior corona filamentous below, plane and lanceolate at apex, up to 1.8 mm. long, up to three-quarters the length of interior corona, transparent, oblong (or subovate), up to 3.7 mm. long, shorter than stamens, acute at apex, the median vein not conspicuously ridge-like, the lateral veins prominent, oblique-ascending; anthers linear-ovate, abruptly apiculate, 1-1.5 mm. long, the filaments 0.7-1.2 mm. long, the stamens about twice length of interior corona; ovaries smooth, distinctly 3-lobed, about 1.3 mm. long, the style crassate, subulate, somewhat constricted at base; capsules striate, elliptic before dehiscence, as much as 1.5 mm. beyond apex of sepals, the carpels acute, somewhat deflexed at dehiscence.

TYPE LOCALITY: Goyas, Brazil.

ILLUSTRATION: Gardn. Hook. Ic. 5(1): *pl. 484*. 1842.

DISTRIBUTION: Known from a few collections in Venezuela, Colombia, Bolivia, and Brazil.

VENEZUELA: Amazonas: Esmeralda, alt. 100 m., *Tate 265* (NY). COLOMBIA: Boyaca: Oracue, *Haught 2707* (US). BOLIVIA: La Paz: Ixiamas, 250 m. alt., *Cardenas 2020* (NY). BRAZIL: Without locality, *Pohl 1263* (F).

As the specific name indicates *S. deflexifolia* is readily distinguished by its deflexed leaf-blades; although this character is found in one other member of the genus *S. amoena*, the two species are readily separated on the basis of floral characters. *S. linearifolia* is undoubtedly most closely related to *S. deflexifolia*, both species having linear stiff leaf-blades, ovoid anthers with



long filaments, and crassate styles. The fact that the flowers are not fascicled, but solitary is suggestive of *S. imthurniana*; however, the flowers of the latter are disposed on peduncles.

It is worthy of note that *S. deflexifolia*, considering its wide geographical distribution in tropical America, has been little collected.

15. *SAUVAGESIA PULCHELLA* Seem. Bot. Voy. Herald 1: 80. 1852. Small herbs, 5–15 cm. high; branches of stem slender, short, the lowermost usually 3–5 cm. from base of stem, arcuate or angular-ascending; leaf-blades usually persisting below middle of stem, subsessile, well spaced, chartaceous, elliptic, about 17 mm. long, 2–4 mm. wide, acute at apex, cuneate at base, the lamina narrow-alate on the very short petiole, the costa prominent above and below, scarcely distinguishable from lamina below, the secondary veins prominent, parallel-ascending; stipules striate, linear- or elliptic-falcate, up to 6 mm. long, the elongate cilia of corpus each with a distinct lateral and median gland; flowers 2–5 per bostryx, fasciculate in uppermost leaf-blades, the pedicels up to 5 mm. long, the articulation-stalks about 1 mm. long, the bracts linear or lanceolate, the margins serrate, ciliate toward base, the cilia not glandular-jointed; sepals equal, lanceolate, 1.5–2.7 mm. long, acute, the margins entire except for a few short cilia toward apex, with or without a distinct terminal cilium, the veins  $\pm$  3; petals elliptic, 1.8 mm. long, tapering gradually above middle, rotund at apex, the veins 3, parallel-ascending; exterior corona absent; segments of interior corona oblong, about 1.5 mm. long, the veins usually parallel-ascending, the median veins more conspicuous and branching freely above middle; anthers subrotund or ovate, about 0.4 mm. long, obtuse or acuminate at apex, seemingly bidentate at apex at dehiscence, the filaments slender, about 0.5 mm. long; ovaries ovate, 0.8–1.5 mm. long, the style short, thick, about 0.5 mm. long; capsule narrow-ovate, almost twice length of sepals.

TYPE LOCALITY: Savannas of Panama.

DISTRIBUTION: Widely distributed through the high savannas of northern South America.

COLOMBIA: El Cauca: Alt. San Francisco, *Andre 2853* (F, NY); Tocota, 1500–1800 m. alt., *Lehman 8965* (NY); Magdalena: Santa Marta near Jeracasea, 1000 m. alt., *H. H. Smith 557* (F, NY). VENEZUELA: Aragua, 760 m. alt., *Llewelyn Williams 10814* (F). BRAZIL: Without locality, *Burchell 6960* (NY).

Although Seemann in his original description of *S. pulchella* notes that it is common in the savannas of Panama, I have not seen additional collections from that area.

16. *SAUVAGESIA TENELLA* Lam. Ill. 2: 119. 1793.

*Sauvagesia nana* Ule, Notizbl. Bot. Gart. Berlin 6: 345. 1915.

*Sauvagesia gracilis* Ule, Notizbl. Gart. Berlin 6: 345. 1915.

*Sauvagesia inconspicua* Dwyer, Lloydia 2: 195. 1939.

Herbs 3–7 cm. high, simple or rarely with apical or basal branches, the stem glandular-smooth, seemingly ribbed; leaf-blades glandular-carnose, sessile, elliptic, 3–8 mm. long, 1.8–3 mm. wide, subacute to obtuse at apex, subcuneate at base, the margins with minute cilia or rarely entire, the secondary veins immersed and evanescent; stipules linear, 1–3 mm. long, the cilia 5–7,

well-spaced and exceeding corpus in length; flowers usually 3 per bostryx, the fascicles 1-2, terminal, subtended by reduced stipulate leaves, the pedicels slender, 6-7 mm. long; sepals herbaceous-green, lanceolate to ovate, 3.2-4 mm. long, setose-aristate at apex, the margins mostly scarious, the veins 3+, ascending; petals pink or white, obovate, 3-5 mm. long, equal to or exceeding sepals in length, usually distinctly clawed at base, the veins evanescent and flabellate; segments of exterior corona absent; segments of interior corona usually oblong, rarely narrow-obovate, usually slightly shorter than stamens, rounded or flat-obtuse at apex, the median ridge not obvious, the dorsal furrow absent, the veins 1-2, ascending, usually branching at middle or above; stamens usually exceeding segments of interior corona in length, up to 2 mm. long, the anthers oblong, obtuse at apex, the filaments shorter or longer than anthers; pistil 1-1.5 mm. long, the ovary ellipsoid or rotund, the style shorter than ovary; capsule equal to or exceeding sepals in length, mostly turgid at base (fig. 1, *n-p*).

TYPE LOCALITY: Tropical America.

ILLUSTRATION: St. Hil. Mém. Mus. Hist. Nat. Paris 11: *pl. 1. B, f. 1-7*, 1824.

DISTRIBUTION: Widely distributed through the savannas of Cuba, Central America, and tropical South America.

CUBA: Cienegueta?, *Combs 439* (NY); Oriente: Sabana San Felipe, *Ekman 2398* (NY); Santa Clara: Manacas, *Leon and Cazanas 5907* (NY); Without locality, *Wright 2131* (NY). GUATEMALA: Narbasco, *Bernoulli 947* (NY). PANAMA: Coclé: *Allen 830* (NY); Pacora and Chepo, *Woodson, Allen, and Seibert 1657* (NY). BRITISH GUIANA: Wichabai, Rupununi River, *A. C. Smith 2309* (NY, type of *S. inconspicua*). BOLIVIA: La Paz: S. Marcos and Rio Branco, *Ule 7880* (F, photo of type of *S. nana*); Rio Branco, *Ule 8119* (F, photo of type *S. gracilis*).

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## A NEW SECTION MICROPHYLLAE IN AGROSTIS

ALAN A. BEETLE

In mentally picturing the genus *Agrostis* (Gramineae) it is easy to fall into the habit of thinking of the glumes as awnless. Shishkin (1934) in keying out of 29 species in the Russian flora definitely states for all "glumes always without awn." The glumes of our commonest American species are awnless. It is then somewhat disconcerting to come upon *A. exarata* Trin. and find that, although the glumes of the typical form are only acute, specimens treated as var. *monolepis* may have glumes rather long-awned (1 mm. or more). To this author's knowledge the only other currently recognized species in *Agrostis* described as bearing an awned glume is *A. hendersonii* Hitchc. The following investigation was undertaken to determine whether there were more than varietal significance to the awned-glumed plants usually placed under *A. exarata* and what could be the position in *Agrostis* of such unusual species, the thought being that they might better fall in *Poly-pogon* where awned glumes are usual.

The type locality of *Agrostis exarata* (Trin. Gram. Unifl. 207. 1824) is Unalaska, where it was collected by Eschscholtz. The latest treatment of Alaskan *A. exarata* (Anderson 1944) gives a description that agrees with those of Scribner and Merrill (1910), the original description, and Trinius' illustration in *Species Graminicum*, vol. 1 (1928). It also agrees with the characters of the widest-ranging segregate of the *A. exarata* complex in North America, which always has been considered, and apparently correctly so, as typical *A. exarata*. Specimens have been collected, according to Hitchcock (1935, 1937) from "Western Nebraska, to Alberta and Alaska, and southward to New Mexico, California, and Mexico." The map 683 in the Hitchcock *Manual* omits a dot for South Dakota, apparently overlooking the report by Rydberg (1896) of its rare cocurrence in the Black Hills. This record has recently been reaffirmed by *Ester Suter* 10, Wind Cave Canyon, Custer County, South Dakota, collected in 1936.

Typically, then, *A. exarata* is a perennial with an awnless lemma (rarely awned and then the awn short and not bent), a prominent palea usually half the length of the lemma, scabrous glumes which are acute but not attenuate, and a narrow slender panicle, the ascending appressed branches floriferous to the base. These characters are well demonstrated in the following collections taken at scattered points throughout the range: TEXAS: *Moore & Steyermark* 3158. ARIZONA: *Thorner* 492. UTAH: *Stanton* 590. NEVADA: *Kennedy* 4068. CALIFORNIA: *Beetle* 3028. OREGON: *Heller* 13056. WASHING-

TON: A. A. & E. G. Heller 4018. BRITISH COLUMBIA: Eastham 9039. In California this species is commonly found at higher elevations, in the northern counties and southward both in the Coast Ranges and the Sierra Nevada to the mountain peaks of the southern counties.

*Agrostis exarata* has not lived up to the suggestion of promise indicated in many early publications of the United States Dept. of Agriculture (Tracy & Nealley 1888, Anderson 1889, Vasey 1889, Scribner 1900, Forest Service 1914). The plate 13 of Tracy & Nealley (which is the same as plate 49 of Vasey) is an excellent illustration of typical *A. exarata* and agrees in all details with the plate of Trinius mentioned above. The plate 106 of Vasey listed as *A. exarata* var. *pacifica* is also good *A. exarata* differing only in the short, unbent, included awn, a sporadically occurring remnant of what was apparently formerly an awned condition or else representing a visible trace of an awned parentage somewhere in the ancestry. Water is too strong a limiting factor in the life history of *A. exarata* to make it more than an ephemeral plant on most of the western range. Failure of the grass when sown on the open range has been reported by Lyon and Hitchcock (1904).

Two California species are closely related to *A. exarata*: the first *A. rossae* Vasey of higher elevations, a dwarf, tufted plant with narrow, crowded basal leaves and awnless lemma; the second, *A. californica* Trin., of coastal bluffs where it is easily marked by its dense, broad panicle and strongly scabrous glumes. These three species probably belong to the section *Trichodium* Michx. of *Agrostis*. For a clearer picture a sectional treatment of *Agrostis* as a whole is needed.

On the other hand the material treated by Hitchcock (1935, 1937) as varieties *monolepis* and *ampla* of *A. exarata* and as *A. hendersonii* differ in a number of respects and are here considered to comprise a separate section, *Microphyllae*, consisting of four species with varieties. From all other species of *Agrostis* this section is separated by the awning of the glumes. From *Agrostis exarata* and relatives, with which they have usually been confused though they are not necessarily closely related, they are separated as follows:

Section *Microphyllae*

*A. exarata*, *A. rossae*, and  
*A. californica*

- |  |   |
|--|---|
| (1) Glumes attenuate-tipped or awn-tipped.                 | (1) Glumes acute.   |
| (2) Lemma with a bent, exserted awn (figs. 1, 2, 6, 7, 8). | (2) Lemma awnless, or with a short, unbent, included awn (figs. 3, 4, 5). |
| (3) Palea absent or obsolete.                              | (3) Palea present and prominent.  |

The chromosome number of typical *A. exarata* Trin. as reported by Nielsen (1939), is  $2n = 28$ . The chromosome number of *A. ampla* Hitchc. (Stebbins 2816, 2953) of Sect. *Microphyllae* is  $2n = 42$  (Stebbins & Love 1941), thus supplying cytological evidence that two specific entities may be involved. Through the kindness of Dr. G. L. Stebbins, Jr. (College of Agri-

culture, University of California) the chromosome number of *A. hendersonii* Hitchc. (*A. microphylla* var. *hendersonii* of this paper) may be reported as  $2n = 42$ . The count was made from material grown in Shasta County, California (*Beetle & Stebbins 3354*).

### Section *Microphyllae* Beetle, sect. nova.

Glumis scabris ad dorso, aristatis; lemmis arista prominenti geniculata exserta munitis; palea nulla.

Two short-lived perennials and two annuals along the Pacific coast of North America.

### KEY TO THE SPECIES

- Glumes 2.75–3 mm. long; lemma 1.5 mm. long; the awn 3 mm. long, bent at the middle. 1. *A. ampla*.
- Glumes 3–6 mm. long; lemma 2–4 mm. long, the awn 3.5–10 mm. long, bent below the middle.
- Stout perennials of moist meadows; panicle open, 1–2 dm. long; basal leaves broad and conspicuous. 2. *A. inflata*.
- Slender annuals of vernal pools; panicle dense, up to 7 cm. long; basal leaves few and ephemeral.
- Lemmas, if pubescent at all, only tufted at base; lemma only shortly toothed at apex.
- Glumes 3–4 mm. long; lemma 2 mm. long, the awn 3.5–4 mm. long. 3. *A. microphylla*.
- Glumes 4–6 mm. long; lemma 3 mm. long, the awn 7 mm. long. 4. *A. microphylla* var. *intermedia*.
- Glumes 7–8 mm. long; lemma 4 mm. long, the awn 10 mm. long. 5. *A. microphylla* var. *hendersonii*.
- Lemmas evenly pubescent over the back; lemma deeply two lobed, the lobes with setaceous teeth 1 mm. long. 6. *A. kennedyana*.

1. *AGROSTIS AMPLA* Hitchc. U. S. Dep. Agr. Bur. Pl. Ind. Bull. **68**: 38. pl. 20. 1905.

Tufted perennial; culms one to many, erect (or somewhat geniculate from the lowest node), up to 6 dm. tall; depending on the habitat the blades mostly basal, or evenly scattered on the culm; blades up to 5 mm. broad, scabrous on the margins and minutely scaberulous on the nerves; panicle typically well-exserted from the upper sheath, about 1 dm. long, the lowest fascicle (ca. 1 cm. long) somewhat remote, the other fascicles about equal and appressed to form a dense panicle; glumes subequal, 2.75–3 mm. long, including the awn (usually ca. 1 mm. long, occasionally prolonged or absent) scaberulous on the midrib and minutely so on the back; lemmas ca. 1.5–2 mm. long, long-awned from a deeply bifid apex, smooth, the callus with two tiny tufts of white hair; awn ca. 3 mm. long, once geniculate at about the middle; palea absent or obsolete; anthers 0.33 mm. long; caryopsis brown, 1 mm. long. (fig. 1.)

TYPE LOCALITY: Oregon, Multnomah County, Rooster Rock, *Suksdorf 135*.

DISTRIBUTION: Washington and Idaho south to California.

WASHINGTON: Clallam Co., Olympic Mts., *A. D. E. Elmer 1953*; Chelhalis Co., Montesano, *A. A. & E. G. Heller 4010*. IDAHO: Elmore Co., Atlanta, *Christ & Ward 8326*.

OREGÓN: Yamhill Co., McMinnville, *Shear* 1633, 1643, 1646, 1650; Oregon City, *Chase* 4935; Klamath Falls, *Hitchcock* 2979. CALIFORNIA: Humboldt Co., *Tracy* 4825, 1754; Sonoma Co., *Yates* 6582; Tulare Co., *Wiggins & Ferris* 2656; Santa Cruz Co., *Howell* 19598.

The names *Agrostis microphylla* Steud. and *A. inflata* Beal are applied to species whose descriptions follow. Discarding the invalid *Agraulus brevifolius* Nees (1857), the next specific name is *Polypogon alopecuroides* Buckl. (1863) which, though validly published, cannot be transferred to *Agrostis* because of the earlier *A. alopecuroides* Lam. (1791). The next name then, is *Agrostis ampla* Hitchc. (1905) which was carefully described and illustrated (see his plate 20). The description and illustration fit the plants which have long passed as an awned variety of *A. exarata* in all but one detail. Hitchcock states that the glumes are "acuminate, but not awn-pointed." Many specimens that fall into this group on all other characters have glumes that are prominently awned. Because of the differences in technical measurements, the usually awned glumes, the minute or absent palea, and the awned lemma, *A. ampla* Hitchc. is taken to represent a distinct species.

The very dense-panicle forms (represented by *Beetle* 2890, *Stebbins* 2958, *Tracy* 14016, and *Shear* 1650) are sporadically occurring and only represent a form which may be treated as: *Agrostis ampla* Hitchc. f. **monolepis** (Torr.) Beetle, comb. nov. [*Polypogon monspeliensis* var. *monolepis* Torr. U. S. Rept. Expl. Miss. Pacif. 5: 366. 1857. *Agrostis exarata* var. *monolepis* (Torr.) Hitchc. Am. Jour. Bot. 21: 136. 1934.]

## 2. AGROSTIS INFLATA Beal, Grasses N. Am. 2: 325. 1896.

Perennial, culms clumped, strictly erect, 5–8 dm. tall; leaves sometimes crowded at the base, basal and culm leaves up to 8 mm. broad, 1–1.5 dm. long, scabrous on the nerves and margins; panicle 1–2 dm. long, often diffuse, the pedicels not always floriferous to the base; awned glumes 4–5 mm. long, scabrous on the midrib; lemma 2 mm. long, glabrous except for two small tufts at the base, the awn 6 mm. long, geniculate below the middle; palea absent. (fig. 2.)

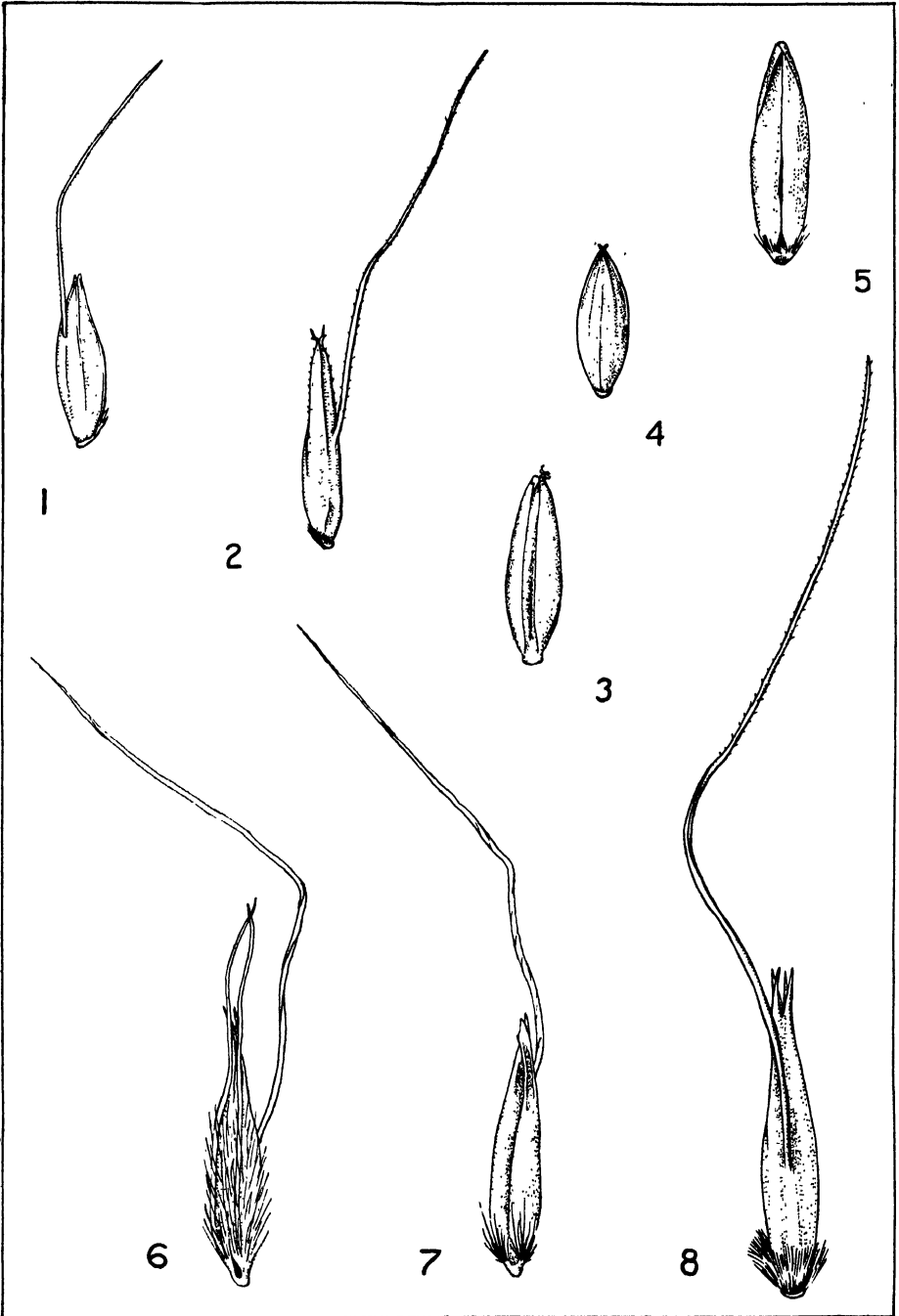
TYPE LOCALITY: Vancouver Island, British Columbia, *Macoun* 258.

DISTRIBUTION: Boggy meadows, coast ranges at low elevations, Vancouver Island, British Columbia south to southern California.

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### Explanation of figures 1–8.

Sample undissected florets of *Agrostis* species, mainly showing the lemma. FIG. 1. *A. ampla*, drawn from *Tracy* 14016. FIG. 2. *A. inflata*, drawn from Mendocino County, Calif., material collected by P. B. Kennedy, May 30, 1929. The sheet is marked in Hitchcock's handwriting "*Agrostis exarata microphylla* (Steud.) Hitchc." and "differs from others in having slender diffuse panicle." FIG. 3. *A. rossae*, drawn from *Baker* 10694. FIG. 4. *A. exarata*, drawn from California material. FIG. 5. *A. californica*, drawn from *Pringle* 12. FIG. 6. *A. kennedyana*, drawn from the type. FIG. 7. *A. microphylla* var. *intermedia*, drawn from the type. FIG. 8. *A. microphylla* var. *hendersonii*, drawn from *Beetle* 3277. The figures drawn by Viola Memmler and Margery P. Mann.



BRITISH COLUMBIA: Vancouver Island, *Macoun* in 1887 (the same as the *Macoun 82* reported by Hitchcock in 1905 as *A. ampla*), *Dawson* in 1885, *Hitchcock 4875*. WASHINGTON: Kitsap Co., *Otis 1644*. OREGON: Polk Co., *Ferris 7790*; Roseberg, *Howell* in 1887; Marshfield, *Haydon*. CALIFORNIA: Del Norte Co., *Yates 5750* and *Davy 5950a*; Humboldt Co., *Tracy 3785, 8271, 8285, 12809, and 13857*; Mendocino Co., *Davy & Blasdale 5199, 5262, 5299, Beetle & Stebbins 3499*; Sonoma Co., *Wagnon 190, 214, Yates 5574, 6565, 6582*; Santa Cruz Co., *Howell 19600*; Marin Co., *Davy 4337*; Monterey Co., *Kennedy* in 1928, *Davy 7506, Heller 6828*; Orange Co., e. of Santa Ana, *Love* in 1942.

The plants of *Agrostis inflata* are in some ways intermediate between *A. microphylla* and *A. ampla*. They have the longer awn and larger glumes of the former but the perennial habit and longer inflorescence of the latter.

### 3. AGROSTIS MICROPHYLLA Steud. Syn. Pl. Gram. 1: 164. 1854.

Annual, loosely tufted, with slender, fibrous roots; culms erect, often branched at the base, slender, smooth, constricted at the black nodes, 1–4 dm. tall; leaves of the culm 2 or 3; sheaths nearly smooth, closed, shorter than the internodes; blades erect, scabrid, flat or loosely involute, 2–5 cm. long; ligule usually lacerate, 2–4 mm. long; inflorescence a close-flowered, spike-like panicle, up to 7 cm. long, light green or purplish, the numerous exserted awns usually giving it a feathery appearance; rays in semiverticillate clusters at the 5–7 nodes, unequal, barely exceeding the intervals, floriferous to the base; glumes 3–4 mm. long, subequal, scabrous on the keel; lemma 2 mm. long, broadly oblong, 4-toothed at the apex, smooth except at the base, thin, obscurely 4-nerved, the awn arising above the middle, geniculate below the middle, hispidulous, slender, 3.5–4 mm. long; palea absent.

TYPE LOCALITY: "in Am. Sptr.," *Douglas*.

DISTRIBUTION: California Coast Ranges, Humboldt Co. south to San Diego Co.

Humboldt Co., *Heller 13772* and *Tracy 13857*; Sonoma Co., *Yates 6550*; Marin Co., *Howell 19479*; San Mateo Co., *Abrams 2458*; San Diego Co., *Orcutt 1176*; and Drews Valley, *Austin & Bruce 1740*.

The earliest specific name applied to a species included in the present section is *A. microphylla* Steud. (1854). Only two years after its original publication in 1856 Torrey identified the name with specimens of *A. ampla* Hitchc. which was then an undescribed species. The application of *A. microphylla* was certainly correctly established in 1893 by Vasey and beautifully illustrated. The plant shown agrees in all respects with the original description of Steudel. Vasey correctly observes in reference to Bolander (1864–1865) and Thurber (1880) that "This species has been referred to *A. exarata*, as it resembles some of the small forms of that variable species, but it may be distinguished by the smaller leaves, slender culms, and long awns." However, the species has continued to be confused with *A. exarata* (and later *A. ampla*) under the influence of Hitchcock (1905, 1912, 1935, 1937) whose too broad interpretation has crossed specific lines. The following specimens which have been cited under *A. microphylla* Steud. are typical of the species: *Orcutt 1176* (Hitchcock 1912), *Davy 5142* (Scribner 1901, Hitchcock 1905), and *Davy 6573* (Hitchcock 1905).



4. *A. MICROPHYLLA* var. *intermedia* Beetle, var. nov.

*Agrostidi microphyllae* affinis sed glumis aristatis 4–6 mm. longis, lemma 3 mm. longa arista 7 mm. longa munita recedit. (fig. 7.)

TYPE LOCALITY: California, Lake County, 2.9 miles north of Middletown, May 11, 1943, *J. T. Howell 18063* (TYPE in the Agronomy Division Grass Herbarium, Univ. of California, Davis, Calif.).

DISTRIBUTION: California, lower elevations away from the coast.

Lake Co., (see type) *Eastwood & Howell 5642*; Napa Co., *Tracy 1856*; Calaveras Co., *Carlson 302, Yates 162*; Merced Co., *Hoover 532a* (reported as *A. hendersonii* by Hoover, 1936).

5. *A. MICROPHYLLA* var. *hendersonii* (Hitchc.) Beetle, comb. nov.

*A. hendersonii* Hitchc. Jour. Wash. Acad. **20**: 381. 1930.

Like typical *A. microphylla* and the var. *intermedia* except for the following measurements: awned glumes 7–8 mm. long, lemma 4 mm. long, conspicuously tufted at the base; awn of the lemma 10 mm. long. (fig. 8.)

TYPE LOCALITY: Oregon, Jackson County, Sams Valley, near Gold Hill, *Henderson 12387*.

DISTRIBUTION: vernal pools, inland, Oregon (type locality) and California.

CALIFORNIA: Shasta Co., *Beetle 3277* (cited in Beetle 1943), *Beetle & Stebbins 3354*; Calaveras Co., *Yates 5162, Carlson 300, 950*.

6. *A. kennedyana* Beetle, sp. nov.

*Agrostidis microphyllae* habitu; culmis ad 2 dm. altis; panícula densa, 1–4 cm. long; glumis imparibus, prima 4 mm. longa, altera 3 mm. longa, callo prominenti; lemma profundissime bifida, aequaliter pubescenti, corpore 1.5–2 mm. longo, lobis dentibus setaceis ca. 1 mm. longis munitis, arista 5–6 mm. longa geniculata e dorso exorienti; palea nulla; caryopsidi 1–1.5 mm. longa. (fig. 6.)

TYPE LOCALITY: California, San Diego County, San Diego, April, 1902, *G. B. Grant 896* (TYPE in the herbarium of the Univ. of California, Berkeley). Only other collection seen: Calif., San Diego Co., La Jolla, May 3, 1914, *F. E. & E. S. Clements 292* (distributed as *Gastridium lendigerum*).

Named for Patrick Beveridge Kennedy who joined the staff of the Agronomy Division, University of California, in January, 1914, moving into the newly completed Hilgard Hall on the Berkeley Campus. For over 15 years he carried out to the fullest the ideal set forth in stone carved letters over the front portal—"to rescue for human society the native values of rural life." Not least in importance among many practical accomplishments was his contribution to the knowledge of California grasses.

The contrasting characters of *Agrostis* and *Polypogon* may be summarized as follows:

<i>Agrostis</i>	<i>Polypogon</i>
(1) Glumes not awned (except Sect. <i>Microphyllae</i> ).	(1) Glumes awned.
(2) Disarticulation above glumes (except <i>A. semiverticillata</i> ).	(2) Disarticulation below glumes.

- |  |  |
|--|--|
| (3) Lemma awn if present often geniculate.                     | (3) Lemma awn never geniculate.  |
| (4) Callus hairs common.                                       | (4) Callus hairs never present.  |
| (5) Lemma awn never terminal.                                  | (5) Lemma awn terminal in Sect. <i>Polygonagrostis</i> .                 |
| (6) Palea often absent (always in Sect. <i>Microphyllae</i> ). | (6) Palea well developed, from one-half as long as to subequal to lemma. |

The awned-glumed species of *Agrostis* Sect. *Microphyllae* might fall into *Polypogon* on character (1), but fall short on the remainder and are better retained in *Agrostis*.

In the preparation of this paper material from the following herbaria has been examined: Agronomy Division Grass Herbarium, College of Agriculture, Univ. of California, Davis; Botany Department, Univ. of California, Berkeley; Dudley Herbarium, Stanford University; California Academy of Sciences; United States National Herbarium. In the interest of brevity the source of the specimens cited, except types, is not further specified.

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## STUDIES IN THE SAPOTACEAE—IV. THE NORTH AMERICAN SPECIES OF *MANILKARA*

ARTHUR CRONQUIST

This paper completes the revision of the North American *Sapotaceae* which I have undertaken under the auspices of the Chicle Development Co. The work has been done under the direction of Mr. B. A. Krukoff, to whom I acknowledge my gratitude for various assistance. I wish also to thank the curators of the several herbaria who have kindly loaned specimens for study. These herbaria are abbreviated hereinafter as follows:

- A—Arnold Arboretum, Harvard University, Jamaica Plain, Mass.
- CR—Museo Nacional de Costa Rica, San José.
- CU—Estacion Experimental Agronomica, Habana, Cuba.
- F—Field Museum (Chicago Natural History Museum).
- G—Gray Herbarium, Harvard University, Cambridge, Mass.
- Mich—University of Michigan, Ann Arbor.
- MO—Missouri Botanical Garden, St. Louis.
- NY—New York Botanical Garden.
- PR—Tropical Forest Herbarium, U. S. Forest Service, Rio Piedras, Puerto Rico.
- US—United States National Herbarium, Washington, D. C.

The genus *Manilkara* was described by Adanson (Fam. Pl. 2: 166. 1763), with a reference to an excellent figure in the pre-Linnaean *Hortus malabaricus*. It was generally reduced to *Mimusops* until revived by Dubard in 1915 (Ann. Col. Inst. Mart. III. 3: 6-28). The first species assigned to it by Dubard was *M. kaukii* (*Mimusops kaukii* L.), and this has generally been considered to be the type. *Manilkara* is well separated from the strictly old-world *Mimusops* by its relatively long and lateral rather than small and basilateral seed-scar, and by having usually 6 sepals instead of 8, with attendant differences in number of corolla-lobes, stamens, and staminodes. Thirty-three species were recognized by Dubard, 13 of them in the new world.

*Muriea*, which has the staminodes replaced by functional stamens, has sometimes been considered distinct from *Manilkara*, but there seems to be no very good reason to believe that its two species, one Antillanean, the other Indian, are closely related. A new genus *Shaferodendron* has recently been segregated by Gilly (Trop. Woods 71: 3-6. 1942), differing from *Manilkara* in its relatively long corolla-tube and short lobes, with the stamens inserted near the middle of the tube instead of at its summit. The difference seems to me of no more than sectional importance at best, especially since Gilly has shown that *Achras*, which sometimes has the corolla-tube longer than the lobes, must be submerged in *Manilkara*.

*Achras* is very similar to *Manilkara* in all significant features except the absence of the dorsal appendages of the corolla-lobes. Gilly has discovered transitional forms, previously identified as *Achras sapota*, in which the dorsal appendages are obviously present, but partly united with the corolla-lobes. Since the separation of the two genera depends solely on the technical character, Gilly's discovery of these transitional forms necessitates their union. As pointed out by Gilly (Trop. Woods 73: 1-22. 1943), the original *Achras* L. is not the same as the group to which the name is now commonly applied, and cannot properly be used for it. The valid name for the genus under discussion is therefore *Manilkara*.

Inasmuch as I have found it necessary to reduce many previously proposed species, some discussion of specific concepts may be in order. My own is moderately conservative, based primarily on morphologic discontinuity, or very strong modal distribution. As in most tropical groups, the material now available for study is frequently insufficient to verify the existence of discontinuity, and I have in certain cases maintained, with appropriate comment, species which may have to be submerged when more material has been accumulated. The names which I have reduced without comment are those which I believe to be based on trivial and inconstant variations.

Our species of *Manilkara* are in general separated by strong floral characters, although they may be vegetatively very similar. Sterile specimens may be difficult or even impossible to determine with certainty, even after one is familiar with the entities involved, except as vegetatively similar species are eliminated by geographic considerations.

The "sapodilla-nispero complex" (species No. 9-12 of this treatment) has recently been revised by Gilly (loc. cit.), who segregated nine new species, based wholly on floral characters, from *Manilkara zapotilla* (*Achras sapota* of auth.). Four of these segregates are here referred back to *M. zapotilla*; the other five are grouped under two of their number, *M. staminodella* and *M. meridionalis*. I am reluctant to recognize specifically plants which are in the herbarium vegetatively apparently identical, but the floral variation within what has been called *Achras sapota* is so great as to demand some sort of segregation until it is conclusively shown that all the variants are parts of a single breeding population. It is interesting and perhaps significant that the sapodilla is divided by the chicleiros into three varieties, but I have not been able to correlate these in the herbarium with the three apparent morphological species. (See Egler, Bull. Torrey Club 71: 235-245. 1944.)

The names nispero and bullet-wood are applied more or less indiscriminately to most of the species. *M. zapotilla*, and its close relatives *M. staminodella* and *M. meridionalis*, are commonly known as sapodilla, but this name, alone or in various combinations or variations, is often used for other species as well. *M. emarginata*, for example, is known in Florida and the Bahamas as wild dilly. *M. bidentata* is often called balata, from its gum.

I have not considered it necessary to repeat all of the older and more obscure synonymy, much of which must in any case be taken to a certain extent on faith. This is available, for those who desire it, in Pierre and Urban's treatment of the *Sapotaceae* of the West Indies (Symb. Ant. 5: 95-176. 1904), and in Gilly's revision of the *Manilkara sapodilla* group (Trop. Woods 73: 1-22. 1942).

#### MANILKARA Adans.

Trees; leaves alternate, exstipulate; primary lateral veins parallel, straight or nearly so, but not especially crowded; reticulum evident (and close) or obscure; flowers perfect, or rarely unisexual; sepals biseriate, commonly 6, occasionally 8, or in one species sometimes 4; corolla-lobes as many as the sepals, each with a pair of dorsal more or less petaloid appendages at the base, or these partly or wholly fused to the lobes, or rarely vestigial; stamens as many as the corolla-lobes and opposite them, alternating with an equal number of staminodes (sometimes nearly obsolete), or these sometimes replaced by functional stamens; ovary about 6-14-loculate; ovules attached laterally; seed-scar relatively long, lateral; endosperm copious.

#### KEY TO THE SPECIES

1. Corolla-lobes and their appendages free nearly or quite to the summit of the tube.
2. Stamens as many as the corolla-lobes and opposite them; staminodes alternate with the corolla-lobes, or obsolete.
3. Corolla-tube not more than about half as long as the lobes, the stamens inserted at its summit; leaves various, but not narrowly oblong except in forms of *M. emarginata*. (*Eumanilkara*.)
4. Appendages of the corolla-lobes about equaling or exceeding the proper lobes; staminodes various.
5. Flowers about 3-10 in a cluster, small, the corolla about 5-7 mm. long; appendages, or some of them, bifid or trifid; fruit smooth or slightly roughened, scarcely mealy; Hispaniola to northern South America and Panama. 1. *M. bidentata*.
5. Flowers about 1-2 in a cluster, large, the corolla about 9-14 mm. long; appendages entire; fruit mealy-roughened.
6. Corolla-lobes and their appendages nearly or quite of the same texture; staminodes nearly as long as the corolla-lobes, about 5-9 mm. long; Puerto Rico and the Virgin Islands. 2. *M. pleeana*.
6. Corolla-lobes conspicuously thinner and softer than their firm thick appendages; staminodes very short, about 1.5 mm. long; Jamaica. 3. *M. excisa*.
4. Appendages of the corolla-lobes not more than about  $\frac{1}{2}$  as long as the proper lobes; staminodes much shorter than the corolla-lobes.
5. Staminodes petaloid, about 3.5-4 mm. long; leaves about 10-20 cm. long, the lower surface generally conspicuously paler than the upper and often rather yellowish; Costa Rica, Jamaica, and apparently Oriente, Cuba.
6. Flowers about 1-3 in a cluster; staminodes broadly obovate to rhombic or ovate, irregularly laciniate-dentate; Costa Rica. 4. *M. spectabilis*.

6. Flowers about 4-6 in a cluster; staminodes lanceolate, entire; Jamaica, and apparently Oriente, Cuba. 5. *M. sideroxylon*.
  5. Stamines thickened, scarcely petaloid, up to about 1.5 mm. long, or obsolete; leaves about 4-10 cm. long, about the same color on both sides, or somewhat redder beneath; Florida; Bahamas; Cuba; Hispaniola. 6. *M. emarginata*.
  3. Corolla-tube several times as long as the lobes, the stamens inserted near the middle; leaves narrowly oblong; Cuba. (*Shaferodendron*.) 7. *M. mayarensis*.
  2. Stamens twice as many as the corolla-lobes; staminodes none; Cuba and Hispaniola. (*Murica*.) 8. *M. albescens*.
  1. Corolla-lobes and their appendages more or less united above the tube, or the appendages apparently wanting (two species, which may have only a short union of the lobes and their appendages, have the corolla-tube  $\frac{3}{4}$  as long to a little longer than the lobes, unlike any of the preceding species). (*Achras*.)
  2. Flowers solitary in the axils; corolla-tube about  $\frac{3}{4}$ -1 $\frac{1}{4}$  as long as the lobes.
  3. Corolla-lobes with evident dorsal appendages broader than and nearly or quite as long as the proper lobes.
  4. Stamines minute, scarcely or not at all petaloid, about 2 mm. long or less, less than half as long as the corolla-lobes. 9. *M. staminodella*.
  4. Stamines well developed, petaloid, about 2.5-6 mm. long, well over half as long as the corolla-lobes. 10. *M. meridionalis*.
  3. Corolla-lobes entire or merely tridentate at the apex, the teeth all in about the same plane, the central one generally the largest. 11. *M. zapotilla*.
  2. Flowers 2-5 in the axils; corolla-tube about  $\frac{1}{4}$ - $\frac{1}{2}$  as long as the lobes; appendages apparently wanting.
  3. Leaves mostly 10-25 cm. long, 3-10 cm. wide, occasionally some of them smaller; continental. 12. *M. chicle*.
  3. Leaves about 4-9 cm. long, 15-27 mm. wide; poorly known plant of Haiti. 13. *M. gonavensis*.
1. MANILKARA BIDENTATA (A. DC.) Chev. Rev. Bot. & Agr. 12: 270. 1932.  
*Mimusops bidentata* A. DC. Prodr. 8: 204. 1844.  
*Mimusops sieberi* A. DC. loc. cit.  
*Mimusops balata* var. *domingensis* Pierre, Bull. Soc. Linn. Paris 64: 508. 1885.  
*Mimusops riedleana* Pierre ex Baill. Bull. Soc. Linn. Par. 2: 922. 1891.  
*Mimusops balata* var. *sieberi* Pierre, Symb. Ant. 5: 166. 1904.  
*Mimusops nitida* Urb. Symb. Ant. 5: 167. 1904.  
*Manilkara riedleana* Dubard, Ann. Col. Inst. Mars. III, 3: 17. 1915.  
*Manilkara nitida* Dubard, loc. cit., p. 18.  
*Mimusops daricensis* Pitt. Contr. U. S. Nat. Herb. 18: 249. 1917.  
*Manilkara darienensis* Standl. Trop. Woods 31: 45. 1932.

Large tree sometimes more than 20 m. tall; leaves mostly narrowly ovate, varying to elliptic, obtuse or broadly rounded to abruptly short-acuminate, about 6-30 cm. long and 3-12 cm. wide, glabrous from the first, or sometimes short-hairy when young, green or slightly reddish beneath, in herbarium specimens, the upper surface green or commonly darkened and somewhat purplish brown; petioles about 1.5-4 cm. long; flowers commonly about 3-10 in a cluster, the glabrous pedicels about 1.5-3 cm. long; sepals about 5-6 mm. long, the outer generally soon glabrate; corolla about 5-7 mm. long, the tube several times shorter than the narrow lobes; appendages about as long and nearly or quite as wide as the corolla-lobes, some or all of them deeply bifid or trifid, often irregularly so; staminodes about 1.5-3.0

mm. long; anthers about 1.8–2.5 mm. long; ovary glabrous, about 6–10-celled; style glabrous, about 4–5 mm. long; fruit globose or ellipsoid-globose, smooth or slightly roughened, but not mealy, about 2.5–3.5 cm. long.

TYPE: *Richard* s.n., French Guiana; photograph in Rev. Bot. & Agr. 12: 269. 1932.

DISTRIBUTION: Hispaniola, Puerto Rico, Lesser Antilles, northern South America, and Panama.

HAITI: *Baker* 7 (US); *Ekman* H2580 (US). DOMINICAN REPUBLIC: *Abbott* s.n. (US), 196 (US); *Ekman* 11184 (US), 15087 (US); *Taylor* 6 (NY). PUERTO RICO: *Britton* 8096 (NY, US), 8111 (NY), *Britton & Brown* 6974 (NY); *Cowles* s.n., (NY); *Gleason & Cook* Q-14 (NY); *Heller* 733 (NY); *Johnston* 517 (NY); *Miller* 1622 (US); *Sargent* 204 (US); *Sintenis* 1422 (MO, NY, US), 5174 (G, US), 6753 (MO, NY); *Stevens & Hess* 2759 (NY); *Stevenson* 1920 (NY, US). ST. JAN: *Britton & Shafer* 574 (NY, US); *White* 1497 (NY, US). TORTOLA: *Beard* 318 (A); *Britton & Shafer* 816 (NY, US); *Fishlock* 471 (NY). GUADELOUPE: *Duss* 3263 (F, MO, NY, US), 4125 (NY, US). DOMINICA: *Hodge* 909 (G). MARTINIQUE: *Duss* 252 (= 4557) (F, G, MO, NY, US); *Hahn* s.n. (G). BARBADOS: *Eggers* 7260 (A, US). PANAMA: *Bocas del Toro*: *Cox* s.n. (US). Panama: *Kluge* 55 (US). CANAL ZONE: *Pittier* 2699 (US), 4318 (G, NY, US), 4384 (US).

This species was long known as *Mimusops balata* (Aubl.) Pierre, or *Manilkara balata* (Aubl.) Dub., based on *Achras balata* Aubl. Aublet confused at least two old-world elements in his diagnosis, however, and it has been claimed (by Chevalier) that he did not even intend to include the native Guiana species to which the name has subsequently been applied. After detailed discussion, Chevalier concluded that the next available name, *Mimusops bidentata* A. DC., should be applied to the Guiana plant, and accordingly transferred it to *Manilkara*. He was followed in this treatment by Eyma (Rec. Trav. Bot. Neerl. 33: 206–7. 1936), but it should be noted that Pierre, on much the same evidence, had earlier reached the opposite conclusion. In view of the fact that the application of Aublet's name is dubious, at best, I think it proper to adopt the next available name, which is *Manilkara bidentata* (A. DC.) Chev.

*M. bidentata* is common and widespread, but does not seem to be unusually variable, at least in North America, and I fail to understand the necessity for the various segregates which have been proposed.

## 2. *Manilkara pleeana* (Pierre) Cronquist, comb. nov.

*Mimusops pleeana* Pierre ex Baill. Bull. Soc. Linn. Par. 2: 923. 1891.

*Achras duplicata* Sessé & Moc. Fl. Mex. ed. 1. 92. 1894.

*Mimusops duplicata* Urb. Symb. Ant. 5: 169. 1904.

*Manilkara duplicata* Dub. Ann. Col. Inst. Mars. III. 3: 14. 1915.

Tree up to about 10 m. tall; leaves narrowly to broadly obovate, or elliptic, broadly rounded to abruptly acuminate at the apex, about 4–20 cm. long and 2–7 cm. wide, about the same color on both sides, or distinctly redder beneath, soon glabrous, borne on petioles about 6–28 mm. long; flowers 1 or 2 in the axils, the pedicels about 1.5–4.5 cm. long; sepals about 8–11 mm. long; corolla about 9–14 mm. long, the lobes several times longer than the tube, the appendages narrower than and about equaling the lobes;



staminodes petaloid, about 5–9 mm. long; anthers about 4–5 mm. long; ovary about 6–12-loculate, its style glabrous, 10–17 mm. long; fruit globose or depressed-globose, brown, mealy-roughened, about 3.5–7 cm. long.

TYPE: *Plée 237*, Puerto Rico, stated to be at the museum of Paris.

DISTRIBUTION: Puerto Rico, especially near the coast, and the Virgin Islands.

PUERTO RICO: *Britton 9775* (NY), *9807* (NY); *Britton & Brown 5907* (NY, US); *Britton & Cowell 1951* (NY, US); *Britton & Shafer 1545* (MO, NY, US), *1552* (NY); *Cowles 351* (NY); *Gleason & Cook B-17* (NY); *Gregory 442* (PR); *Holdridge 28* (NY, PR); *Shafer 2639* (NY, US); *Sintenis 3829* (G, MO, NY, US), *5767* (G), *6669* (G, MO, NY, US). TORTOLA: *Fishlock 92* (NY). ST. JAN: *Eggers s.n.* (March 8, 1877) (G, NY).

The date given for *Achras duplicata* Sessé & Moc. is taken from a notation in the New York Botanical Garden copy of the flora, by Dr. John Hendley Barnhart, bibliographer emeritus.

### 3. *Manilkara excisa* (Urb.) Gilly MS in herb., comb. nov.

*Mimusops excisa* Urb. Symb. Ant. 5: 459. 1908.

Tree sometimes 20 m. tall; leaves elliptic or elliptic-obovate, about 8–22 cm. long and 5.5–13 cm. wide, very firm, broadly obtuse to rounded or emarginate at the apex, glabrous, about the same color on both sides, or generally distinctly yellower beneath, borne on petioles about 2–4 cm. long; flowers 1 or 2 in the axils, the stout pedicels about 2–3 cm. long; sepals about 8–9 mm. long, thick and firm; corolla about 10 mm. long, the tube 3.5 mm. long, thick and firm; corolla-lobes thin, shorter than their thick and firm appendages; staminodes broad, thick, about 1.5 mm. long; anthers about 3.5–4.0 mm. long; ovary about 11-loculate, its style glabrous, 7 mm. long; fruit globose or depressed-globose, up to about 4 cm. long or perhaps more, brown, mealy-roughened.

TYPE: Not specified, from among *Sintenis 8765*, *8813*, and *8961*, all from near Troy, Jamaica. Since only No. *8961* is flowering, and the species is founded largely on floral characters, that number may well stand as the type (NY).

DISTRIBUTION: Known only from the type locality, near Troy, Jamaica.

JAMAICA: *Britton 586* (NY); *Sintenis 8765* (NY), *8813* (NY).

### 4. *MANILKARA SPECTABILIS* (Pitt.) Standl. Trop. Woods 31: 45. 1932.

*Mimusops spectabilis* Pitt. Contr. U. S. Nat. Herb. 13: 465. 1912.

Similar to *M. sideroxylon*, sometimes 40 m. tall; flowers mostly 1–3 in the axils; sepals relatively broader, ovate or oblong-ovate; staminodes ovate to rhombic or obovate, erose-laciniate; ovary 10-celled.

TYPE: *Pittier 16012*, Puita, near Port Limon, Limon, Costa Rica, September, 1899 (G, NY, US).

DISTRIBUTION: Known only from the type collection, Limon, Costa Rica.

This species is very similar to *M. sideroxylon*, and may not be distinct. The available material of both species is inadequate, and, in view of their geographic separation, I am reluctant to combine them at this time.

5. *MANILKARA SIDEROXYLON* (Griseb.) Dubard, Ann. Col. Inst. Mars. III. 3: 15. 1915.

*Achras sideroxylon* Hook. Rep. Par. Exh. 3: 61. 1856, hyponym.

*Sapota sideroxylon* Griseb. Fl. Br. W. Ind. 399. 1861.

*Mimusops sideroxylon* Pierre, Not. Bot. Sapot. 37. 1891.

*Mimusops jamaicensis* Pierre, Symb. Ant. 5: 176. 1904.

Tree up to nearly 25 m. tall; leaves rather narrowly elliptic or sometimes elliptic-oblongate, glabrous, or more or less white-sericeous-strigose beneath, about 10–20 cm. long and 3–7 cm. wide, broadly rounded to obtuse or acutish, the lower surface commonly paler than the upper, often yellowish; flowers mostly about 4–6 in a cluster, the pedicels 1–2 cm. long; sepals about 6–7 mm. long, lance-ovate; corolla about 8 mm. long, the tube half as long as the lobes, which evidently exceed their appendages; anthers about 3.5 mm. long; staminodes lanceolate, entire or nearly so, about 4 mm. long; ovary about 6–9-loculate, its style glabrous, about 6 mm. long; fruit brown, mealy-roughened, globose or ellipsoid-globose, about 2 cm. long.

TYPE: Grisebach mentions collections by *McNab* and *March*, in that order, from Jamaica.

DISTRIBUTION: Jamaica, and apparently Oriente, Cuba.

JAMAICA: *Britton* 1644 (NY); *Harris* 5379 (A, G, NY), 9845 (NY, US); *March s.n.* (G). CUBA: Oriente: *Ekman* 16143 (NY, US).

Sterile specimens are distinguished only with difficulty from *M. zapotilla*, but have the leaves paler beneath, and without the loose rufous tomentum which generally persists for a time along the midrib of the latter.

6. *MANILKARA EMARGINATA* (L.) Britt. & Wils. Bot. Puerto Rico 6: 366. 1926.

Large shrub or small tree commonly 4–10 m. tall; leaves short-petiolate, about 2–10 cm. long and 7–45 mm. wide, mostly 1.5–4 times as long as wide, elliptic or oblong, obtuse to more commonly broadly rounded or emarginate, rufous-pubescent beneath when young, generally soon glabrate, about the same color on both sides or distinctly redder beneath, the veiny reticulum evident or obscure; flowers about 1–3 in the axils, the pedicels about as long as the petioles, or longer; sepals about 4–10 mm. long; corolla about 4.5–10.5 mm. long, the lobes narrow, 2–4 times as long as the tube, the appendages about  $\frac{1}{3}$ – $\frac{2}{3}$  as long as the lobes; anthers about 1.8–3.9 mm. long; staminodes thickened, scarcely petaloid, up to about 1.5 mm. long, or nearly obsolete; ovary 6–12-loculate; style glabrous or more or less pubescent below; fruit obovate to spherical or depressed-globose, mealy-roughened, about 1.5–3.5 cm. thick.

TYPE: Description and figure in Catesby, Nat. Hist. Car. 2: 87. 1733. Andros, Bahama Islands.

DISTRIBUTION: Southern Florida, Bahama Islands, Cuba, Hispaniola, and reputedly western Puerto Rico.

Four fairly well marked phases of this species may be recognized. Because of the paucity of flowering material of two of these, it seems unwise to attempt to construct a key. Except in parts of Oriente, Cuba, no more than one subspecies is known to occur in any given region.

6A. *MANILKARA EMARGINATA* (L.) Britt. & Wils. subsp. *typica* Cronquist, subsp. nov.

*Sloanea emarginata* L. Sp. Pl. 512. 1753, sensu stricto.

*Mimusops parvifolia* Radik. Sitzb. Akad. Wiss. München 12: 344. 1882.

*Mimusops floridana* Engl. Bot. Jahrb. 12: 524. 1890.

*Mimusops sieberi*, misapplied by auth. and in herbaria, not A.DC.

Leaves about 3–10 cm. long and 1.5–4.5 cm. wide, mostly 1.5–2.5 times as long as wide, borne on petioles about 5–25 mm. long; corolla about 6–10.5 mm. long, the tube about  $\frac{3}{4}$ – $\frac{1}{4}$  as long as the lobes; ovary consistently about 6-celled, its style glabrous or strigose-puberulent, about 6–13 mm. long. Florida and the Bahamas. An abundance of material of this subspecies has been available from Florida and the Bahama Islands. Since only one other species, *M. zapotilla*, occurs in the area, citations seem unnecessary.

6B. *MANILKARA EMARGINATA* (L.) Britt. & Wils. subsp. *wrightiana* (Pierre) Cronquist, comb. nov.

*Mimusops wrightiana* Pierre, Symb. Ant. 5: 171. 1904.

*Mimusops grisebachii* Pierre, loc. cit., p. 173.

*Manilkara wrightiana* Dubard, Ann. Col. Inst. Mars. III. 3: 16. 1915.

*Manilkara grisebachii* Dubard, loc. cit., p. 15.

*Mimusops camagueyensis* Urb. Rep. Sp. Nov. 24: 8. 1927.

*Manilkara howardii* Gilly, Trop. Woods 74: 15. 1943.

Similar to subsp. *typica*, but the ovary consistently about 9–12-celled, and the style commonly tomentose-puberulent toward the base. Habana to Camaguey and occasionally overlapping into Oriente, Cuba.

TYPE: *Wright 2917*, Cuba (G, MO).

CUBA: *Wright 2927* (G, MO). Habana: *Ekman 13580* (A, F, G, MO); *Leon & Roig 11516* (NY). Matanzas: *Acuña 4479* (CU); *Ekman 16515* (NY, US). Santa Clara: *Britton & Wilson 5662* (NY), *5723* (NY, US), *5748* (NY); *Cuesta 176* (NY); *Howard 5423* (G, NY); *Jack 5137* (A); *Ekman 19071* (F, US); *Leon 11594* (NY); *Roig 924* (NY); *Shafer 340* (NY, US), *421* (G, MO, NY), *2911* (NY). Oriente: *Ekman 4593*, Cauta River (US), *7449*, border of Camaguey (G, NY), *14952* (US); *Roig 5103*, Puerto Padre (CU).

6C. *MANILKARA EMARGINATA* (L.) Britt. & Wils. subsp. *jaimiqui* (Wright) Cronquist, comb. nov.

*Mimusops jaimiqui* Wright in Griseb. Cat. Pl. Cub. 64. 1866.

*Manilkara jaimiqui* Dubard, Ann. Col. Inst. Mars. III. 3: 16. 1915.

Leaves about 2–6 cm. long and 7–20 mm. wide, mostly 2.5–4 times as long as wide, or the smaller ones sometimes proportionately broader, borne on petioles about 4–10 mm. long; corolla about 5 mm. long, the tube  $\frac{3}{4}$ – $\frac{1}{4}$  as long as the lobes; ovary about 7–8-celled, its style mostly glabrous; limits of floral variation unknown. Isla de Pinos, Pinar del Rio, and Oriente, Cuba.

TYPE: *Wright 2918*, prope Chacco de Toro, western Cuba (G, MO, NY, US).

CUBA: *Van Hermann s.n.* (NY). Isla de Pinos: *Britton & Wilson 14362* (NY, US); *Ekman 12011* (US). Pinar del Rio: *Britton & Cowell 9997* (NY, US); *Britton & Gager 7016* (NY); *Ekman 11199* (F), *12688* (US), *12986* (NY), *17382* (NY); *Roig 6540* (CU); Oriente: *Ekman 4790* (G), *7600* (US), *9686* (G), *15390* (NY); *Roig 90* (NY), *6594* (CU).

6D. *MANILKARA EMARGINATA* (L.) Britt. & Wils. subsp. *haitensis* Cronquist, subsp. nov.

Leaves about 3–11.5 cm. long and 1–3.5 cm. wide, mostly 2–3 times as long as wide, borne on petioles up to 10 mm. long; corolla scarcely 5 mm. long, the tube about  $\frac{1}{2}$ – $\frac{3}{4}$  as long as the lobes; ovary about 6–7-celled, its style puberulent below, about 4 mm. long; limits of floral variation not yet established. A subsp. *jaimiqui* differt foliis usque ad 11.5 cm. longis 3.5 cm. latis, tubo corollae pro rata longiore. Hispaniola.

TYPE: *Eyderdam 262*, Les Abricots, Gonave Island, Haiti, August, 1927 (NY); isotypes, G, US.

HAITI: *Ekman H2891* (US), *H8695* (US). DOMINICAN REPUBLIC: *Ekman 11326* (US), *15784* (US); *Holdridge 503* (PR).

*Manilkara grisebachii*, as represented by the type collection, has more tapering leaves and a slightly different aspect than subsp. *wrightiana*, and may eventually prove to be taxonomically separable.

It will be noted that subsp. *jaimiqui* is not known to occur in the intervening area between Oriente and Pinar del Rio, while subsp. *wrightiana* neatly fills the gap, also occasionally overlapping into Oriente. This peculiar distribution of subsp. *jaimiqui*, while interesting and unexplained, is not unique. *Bumelia conferta* is known from several collections in Oriente, and several in Pinar del Rio, but not between, and *Dipholis cubensis* likewise occurs in both Pinar del Rio and Oriente, without having been found in the other provinces. *Manilkara albescens* shows a similar disjunct distribution, but extends eastward from Pinar del Rio into Habana. In each of these cases, sufficient material has now been obtained to suggest that the apparent gap is a real one, and is not likely to be filled in by future collections.

The prominence of the close veiny reticulum, and the degree of reddishness, of the lower surfaces of the leaves, are variable in *M. emarginata*, and some segregates have been proposed on these bases, but the variation is continuous, and these characters are in my opinion quite without taxonomic significance in this instance.

#### 7. *Manilkara mayarensis* (Ekm.) Cronquist, comb. nov.

*Mimusops mayarensis* Ekm. ex Urb. Symb. Ant. 9: 418. 1925.

*Shaferodendron mayarensis* Gilly, Trop. Woods 71: 4. 1942.

*Shaferodendron moaensis* Gilly, loc. cit.

Shrub or small tree up to 10 m. tall; leaves narrowly oblong, about 1–10 cm. long and 5–20 mm. wide, retuse, firm, scarcely or obscurely veiny, glabrous above, provided beneath with a very fine and close wax-impregnated rufous sericeous tomentum, which turns paler with age, the individual hairs often indiscernible under 25 diameters magnification; petioles about 2–12 mm. long; flowers solitary in the axils, on glabrous pedicels about 2–4 cm. long, 6-merous or sometimes only 4-merous throughout; sepals about 6–9 mm. long, the outer glabrous, the inner pulverulent; corolla about 9–11 mm. long, the lobes only about 1.5–2 mm. long, about equaling their dorsal appendages; filaments about 1 mm. long, attached near the middle of the corolla-

tube; anthers about 2.5–3 mm. long; staminodes linear-subulate or linear-lanceolate, about 1 mm. long, inserted at the level of the stamens or at the summit of the corolla-tube, or wanting; style about 10 mm. long; mature fruit unknown.

TYPE: *Ekman 9515*, in Sierra de Nipe ad Rio Piloto in carrascales, Oriente, Cuba.

DISTRIBUTION: Oriente, Cuba.

CUBA: Oriente: *Bucher 11103* (CU); *Ekman 15053* (NY, US); *Boig 1550* (CU, NY); *Shafer 4214* (NY, US), *8298* (NY, US).

Gilly's segregate, *Shaferodendron moaensis*, differs from the type in having the flowers 4-merous instead of 6-merous, but is otherwise very similar and probably represents a mere casual variant. Only a very few flowers of the species are available, so it is difficult to estimate the relative abundance of the 4-merous form.

The isotypes of *M. emarginata* subsp. *jaimiqui* at the Missouri Botanical Garden and the Gray Herbarium contain also pieces of *M. mayarensis*. If these latter specimens came from Pinar del Rio, as did the rest of the collection, the number of Sapotaceae known to occur in Oriente and Pinar del Rio, but apparently not in the intervening provinces, will be increased to five.

## 8. *Manilkara albescens* (Griseb.) Cronquist, comb. nov.

*Bassia albescens* Griseb. Cat. Pl. Cub. 164. 1866.

*Mimusops albescens* Hartog, Trim. Journ. Bot. 17: 358. 1879.

*Murica albescens* Hartog ex Baill. Hist. Pl. 11: 269. 1891.

*Mimusops azulensis* Urb. Symb. Ant. 9: 418. 1925.

*Murica eyerdamii* Gilly, Trop. Woods 71: 5. 1942.

Tree about 6–10 m. tall; leaves about 6–17 cm. long, 2.5–6 cm. wide, mostly elliptic or elliptic-oblong, broadly rounded to occasionally acute or even acuminate at the apex, provided beneath with a very fine and close somewhat waxy sericeous pubescence, which may be pallid, rufous, or so obscure as to escape observation under less than 25 diameters magnification; petioles about 6–30 mm. long; flowers about 2–8 in the axils or at defoliated nodes, the pedicels about 12–18 mm. long; sepals about 4–5 mm. long, all closely sericeous-tomentose; corolla about 6–6.5 mm. long, the tube  $\frac{1}{2}$ – $\frac{1}{2}$  as long as the lobes, the lateral appendages about equaling the lobes; stamens twice as many as the corolla lobes, all antheriferous, the anthers about 2 mm. long or less; staminodes absent; ovary about 6–10-loculate, its style about 3.5 mm. long; fruit globose, about 12–16 mm. thick, mostly 1–2-seeded; seeds about 10–12 mm. long, with a conspicuous cicatroid ventral flange.

TYPE: *Wright 2919*, western Cuba, near Retiro (G, NY, US).

DISTRIBUTION: Pinar del Rio, Habana, and Oriente, Cuba, and Hispaniola.

CUBA: *Cowles 1189* (NY). Pinar del Rio: *Britton 10006* (NY); *Ekman 12982* (NY); *Hermann 607* (CU); Habana: *Ekman 13707* (US). Oriente: *Ekman 15866* (NY), *4376* (US). HAITI: *Ekman 3363* (US), *H8347* (US), *H3317* (US); *Eyerdam 233* (G, NY, US). DOMINICAN REPUBLIC: *Ekman 12065* (US); *Scarff 18E* (F).

9. *MANILKARA STAMINODELLA* Gilly, Trop. Woods **73**: 10. 1943.

*M. striata* Gilly, loc. cit., p. 11.

Similar to *M. zapotilla*; leaves about 5–14 cm. long, 2.5–4.5 cm. wide; corolla-tube more or less pubescent, from about  $\frac{3}{4}$  to fully as long as the lobes; corolla-lobes and their dorsal appendages subequal, united for about  $\frac{1}{2}$  their length, the lobes oblanceolate or spatulate and narrower than their lanceolate or ovate appendages, but all of nearly the same texture; staminodes minute, about 1–2 mm. long, entire or bifid, scarcely or not at all petaloid, reflexed or sometimes erect; ovary about 6–9-loculate; fruit unknown.

TYPE: *Schipp 1310*, Camp 33, British Honduras-Guatemala survey, 2850 feet alt., April 29, 1934 (A, F, G, MO, NY).

DISTRIBUTION: British Honduras, and El Peten, Guatemala.

BRITISH HONDURAS: *Stevenson s.n.*, Chiquibul River, 1926 (US).

10. *MANILKARA MERIDIONALIS* Gilly, Trop. Woods **73**: 12. 1943.

*M. meridionalis* var. *meridionalis* Gilly, loc. cit., p. 13.

*M. meridionalis* var. *caribbensis* Gilly, loc. cit., p. 13.

*M. tabogaensis* Gilly, loc. cit., p. 10.

*M. rojasii* Gilly, loc. cit., p. 11.

Similar to *M. zapotilla*; leaves about 7–13 cm. long, 3.5 cm. wide; corolla-tube glabrous or pubescent, from about  $\frac{2}{3}$  as long to a little longer than the lobes; corolla-lobes and their dorsal appendages subequal, or the appendages longer, united for about  $\frac{1}{3}$ – $\frac{2}{3}$  their length, the lobes oblanceolate or spatulate, generally narrower than their mostly lance-ovate to elliptic or obovate appendages, but all nearly of the same texture; staminodes well developed, petaloid, about 2.5–6 mm. long, more than half as long as the corolla-lobes; fruit brown, strongly mealy-roughened, ovoid or subglobose, up to 3.5 cm. long or perhaps more; seed-scar extending from near the base to well beyond the middle of the strongly compressed seed.

TYPE: *Biolley 17308*, Esparta, Punta Arenas, Costa Rica, February, 1909 (NY—photo, US).

DISTRIBUTION: Guerrero, Mexico, to Colombia and Venezuela; also, probably as an introduction, in Cuba and St. Croix, and perhaps elsewhere in the West Indies.

MEXICO: *Liebmann 304* (A). Guerrero: *Palmer 71*, Acapulco (A, G, MO). COSTA RICA: Punta Arenas: *Biolley 2023* (US). San José: *Rojas 524* (F, CR, MO, NY). PANAMA: *Hayes 793* (NY). Panama: *Standley 27099* (US); *Woodson, Allen & Seibert 1455* (A, MO, NY). CUBA: Pinar del Rio: *Britton & Cowell 9991* (G, NY, US). ST. CROIX: *Thompson 960* (NY).

11. *MANILKARA ZAPOTILLA* (Jacq.) Gilly, Trop. Woods **73**: 20. 1943.

*Achras zapota* of authors, not L. 1753.

*Achras zapota*  $\beta$  *zapotilla* Jacq. Stirp. Am. 57. pl. 41. 1763.

*Achras zapotilla* Nutt. N. Am. Sylva 3: 28. 1849.

*Manilkara calderonii* Gilly, Trop. Woods 73: 18. 1943.

*M. consattii* Gilly, loc. cit.

*M. gaumeri* Gilly, loc. cit., p. 19.

*M. breviloba* Gilly, loc. cit., p. 19.

Large tree sometimes 40 m. tall; leaves clustered toward the ends of the twigs, elliptic or nearly so, rounded to acuminate at the apex, mostly 5–15

cm. long and 2–6 cm. wide, loosely rufous-tomentose beneath when young, soon glabrate, or more tardily so along the midrib, about the same color on both sides, borne on petioles about 1.5–3 cm. long; flowers solitary in the axils, the pedicels nearly as long as the petioles, or a little longer; sepals about 6–10 mm. long; corolla about 5–13 mm. long, the tube  $\frac{2}{3}$ – $1\frac{1}{2}$  as long as the lobes, glabrous or slightly hairy; corolla-lobes entire, irregularly toothed, or shallowly tridentate at the apex, the teeth all in about the same plane, the central one generally the largest; staminodes petaloid, about equaling the lobes; anthers about 1–3 mm. long; ovary about 9–12-loculate, densely short-hairy; fruit brown, mealy-roughened, ellipsoid, ovoid, or subglobose, variable in size, sometimes 10 cm. thick; seeds strongly compressed, commonly 16–23 mm. long and 8–16 mm. wide, the linear scar extending from near the base to beyond the middle, sometimes nearly to the top.

TYPE: Description and figure in Browne's Civil & Natural History of Jamaica, p. 200, pl. 19.

DISTRIBUTION: Widely distributed from southern Mexico to northern South America, and from southern Florida through the West Indies, but probably native only on the continent, from Mexico to Costa Rica.

A series of representative specimens has been cited by Gilly; further citation seems superfluous.

## 12. MANILKARA CHICLE (Pitt.) Gilly, Trop. Woods 73: 14. 1943.

*Achras chicle* Pitt. Jour. Wash. Acad. Sci. 9: 436. 1919.

*Achras calcicola* Pitt. loc. cit., p. 438.

*Manilkara calcicola* Gilly, Trop. Woods 73: 15. 1943.

*Manilkara calcicola* var. *columbiana* Gilly, Trop. Woods 73: 17. 1943.

Tree up to 40 m. tall; leaves oblanceolate or elliptic-oblanceolate to occasionally elliptic or narrowly obovate, mostly 10–25 cm. long and 3–10 cm. wide, some of them occasionally a little smaller, broadly rounded or obtuse to sometimes acuminate, usually conspicuously paler and more yellowish beneath than above, also very finely and closely sericeous-strigose beneath when young, but eventually glabrate; flowers about 2–5 in the axils, the pedicels about 15–30 mm. long; sepals about 5.5–9 mm. long, sericeous-tomentose; corolla about 4.5–8 mm. long, the tube  $\frac{1}{2}$ – $\frac{1}{3}$  as long as the lobes; dorsal appendages wanting; anthers about 3 mm. long; staminodes petaloid, erose, lacinate, or bifid, about 2.5–4.5 mm. long; from scarcely more than half as long to about as long as the corolla-lobes; ovary 6–10-loculate; fruit subglobose or obovoid, about 1.5–4 cm. long, brown and mealy roughened; seed-scar narrow and lateral, but scarcely extending to the middle of the strongly compressed seed.

TYPE: *Pittier 8537*, Vega Grande, near Los Amates, Izabal, Guatemala, May, 1919 (G, NY, US).

DISTRIBUTION: Oaxaca, Mexico, through Central America to Colombia.

MEXICO: Oaxaca: *Llewellyn Williams 9574* (A), *9432* (A, US). BRITISH HONDURAS: *Gentle 3186* (A, Mich, NY); *Lundell 689* (A, Mich); *Record 54* (US); *Schipp 1264* (A, G, Mich, MO, NY); *Walter s.n.* (April, 1915) (G, US). GUATEMALA: Izabal: *Whitford & Stadtmiller 75* (G, US). EL SALVADOR: *Calderon 320* (NY, US), *1371* (US), *2052* (US), *2215* (US). COSTA RICA: Guanacaste: *Cooper 10382* (US); *Standley & Valerio 45660* (US), *48582* (US), *48791* (US). CANAL ZONE: *Pittier 3457* (G, NY, US); *Standley 26384* (US). PANAMA: Darien: *Pittier 5698* (G, NY, US).

13. **Manilkara gonavensis** (Urb. & Ekm.) Gilly MS in herb., comb. nov.

*Mimusops* ? *gonavensis* Urb. & Ekm. Ark. Bot. 22A(17): 76. 1929.

Large tree; leaves elliptic-oblongate, about 4–9 cm. long and 15–27 mm. wide, rounded or retuse at the apex, glabrous above, obscurely sericeous-strigose and sometimes reddish beneath, probably eventually glabrate; petioles about 7–20 mm. long; flowers about 4 in the axils, the pedicels 10–13 mm. long; sepals about 5 mm. long, the outer broader and firmer than the inner; corolla about 5.5 mm. long, the tube a little more than  $\frac{1}{2}$  as long as the lobes; dorsal appendages apparently wanting; staminodes about as long as the corolla-lobes, but narrower; anthers about 2 mm. long; style about 3.5 mm. long; fruit unknown.

TYPE: *Ekman H8741*, base of Morne Fort-Couer, 200 m., Gonave Island, Haiti, July 29, 1927 (US).

DISTRIBUTION: Known only from the type collection, Gonave Island, Haiti.

Only fragmentary flowers of this species were available to Urban, and there is some doubt as to the proper interpretation of these, but they seem unquestionably manilkaroid. The isotype at US, the only specimen available to me, is sterile.

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## THE EFFECT OF COLCHICINE AND ACENAPHTHENE IN COMBINATION WITH X-RAYS ON PLANT TISSUE—I. INTRODUCTION<sup>1</sup>

MICHAEL LEVINE<sup>2</sup>

Colchicine, the alkaloid extracted from the seed or corm of *Colchicum autumnale* L., the meadow saffron, has been known for many years. Houdé isolated this substance in 1887 as a yellow, flocculent material soluble in cold water, alcohol, and chloroform. When injected into the body in small doses, it produces gastrointestinal symptoms, such as vomiting and diarrhea, and in some respects behaves like muscarine, pilocarpine, physostigmine, and snake venom. The early uses of colchicine are given by Lits and his associates (1938a,b) to which the reader is referred.

Dustin (1934) investigated the action of colchicine on karyokinesis and cytokinesis in tumor tissue, and his papers resulted in the development of a number of lines of experimental study, effective in producing genetic changes in plants; the chromosome number in plants has been polyploidized and mutations have been produced at will. Colchicine has been used, furthermore, as a device to facilitate the study of the effects of hormones on various tissues of the animal body, and as an aid in cytological studies. It has stimulated interest in a search for other chemicals that affect the normal processes in nuclear and cell divisions and, finally, coupled with x-ray irradiation it has been used as a therapeutic agent in the treatment of cancer in man and the lower animals, and of bacterial overgrowths on plants.

These different phases of the colchicine literature have been reviewed (Levine 1945a,b), but the large number of reports on colchicine now extant make it impracticable to include all in a general survey. Hence only the salient features of the problem will be mentioned here, and emphasis given to those studies that deal with the effects of colchicine alone or in combination with x-rays on animal and plant hyperplasias.

The early studies on the effects of colchicine on cancer were fragmentary and without experimental basis. The belief that colchicine is an ameliorative in cancer seems to have been derived from some observations on gouty patients who were suffering concurrently from cancer. It was asserted that these patients showed improvement and that the cancerous condition was arrested after treatment with colchicine. Dixon and Malden (1908) were the first to

<sup>1</sup> This work will appear in three parts; a list of literature cited will be found in part III.

<sup>2</sup> Valuable assistance was rendered by Samuel Markowitz and Eleanor Acham, R.N.

study the pharmacological properties of colchicine on the blood and bone marrow of rabbits, rats, dogs, and in one or two instances of man. Rabbits injected subcutaneously with colchicine showed transient leucopenia, and a diminution in the polymorphonuclear cells. The administration of large doses of colchicine caused the appearance of abnormal cells, and normoblasts were commonly found. Bone marrow elements were observed in the general circulation and marrow smears showed an abundance of mitotic cell divisions.

The study of the mechanism of nuclear and cell division and attempts to alter their course have been in progress for many years. In 1933(a,b) Dustin and Grégoire studied the effects of various compounds on mitosis in mouse sarcoma 180. Dustin (1934) continued these studies using tryptaflavine, rivanol, isamine blue, malachite green, arsenicals, benzol, iodine, zinc, mercury, thallium, and certain microbic toxins which he described as karyoklastic agents, and showed that colchicine has a stimulating effect on cell division much like that produced by sodium cacodylate. The number of nuclear divisions was calculated to be 15 times as great as that in untreated tumor tissue. These divisions were followed by karyorrhexis. Colchicine produced the maximum number of division stages in the sarcoma at the ninth hour after injection. Similar reactions were observed in the Kupffer cells, reticuloendothelial cells, the megocytes, and testicular cells.

Dustin (1937) studied further the effects of numerous substances on cell division and suggested they could be arranged in two classes: The first he characterized as having essentially an inhibiting effect on karyokinetic division that resulted in "karyoklastic shock." Substances in the cacodylate group he considered to be powerful excitants of mitotic division. He described the cytoplasm of these cells as turgescent; the prophase stages as of short duration, followed by atypical metaphase stages. The prolonged metaphase stage, which was characteristic of colchicine treatment, showed chromosomes condensed into compact masses, which he described as "radiomimetic." These mitoses either disintegrated, or were completed without the aid of spindle fibers. This division was frequently followed by the development of "monstrous" nuclei. Dustin believed that malignant cells are highly sensitive to this alkaloid. He (1938) showed, too, that the dosage of colchicine required to bring about extreme mitotic activity in tissues of the mouse was a very small fraction of that required for cacodylate. He found that the reaction occurred principally in the generative zone, or in cells made to divide by various means such as trauma, inflammation, carcinogenic activity, or hormones. Achromatic figures, asters, and spindles were totally lacking in these "colchicized" cells. While some cells showed complete pycnosis, normal telophase stages and cytososes occurred. Some cells assumed normal telophase stages and formed giant or polyploid nuclei. Dustin proposed the name of "stathmocinesis" for this type of indirect division, and applied the name

"stathmocinetic poison" to colchicine. He contended that the arrest of nuclear division in the metaphase was preceded by a phase of excitation that distinguished this poison from those that merely inhibited division.

**Effect of Colchicine on Plants.** Havas (1937a), one of Dustin's collaborators, studied the effect of colchicine on plants inoculated with *Bacterium tumefaciens*, an organism that induces crown-gall. He observed that colchicine stimulated the appearance of tumors, but found when the end results were examined that tomato stems treated with colchicine bore tumors that were but half the weight of those in the controls. This led him to believe that colchicine is detrimental to the general development of the plant. Tomato crown-galls painted with a mixture of lanolin and colchicine were reduced in weight as compared with the controls. In *Pelargonium* stems there was no effect on the size of the tumor. *Begonia* stems, covered over a scarred area of about 1 cm. with a mixture of lanolin and colchicine, were stimulated to development in the area, while similar treatment of *Impatiens* proved toxic in some cases; the resistant stems, however, produced adventitious roots. Havas (1937b) studied further the effects of colchicine on germinating seeds and seedlings of a pure line of "Wilhelminia" wheat. Roots and root-hair development were stimulated at first, but the effects were followed by a depression of the growth rate and finally by complete arrest. Colchicine effects were shown in these seedlings by the development of bulbous hypertrophy of the root-tips and the liquefaction of certain parenchymatous elements. Havas (1938) later attempted to show that colchicine effects are of a hormonal nature, as evidenced by the appearance of adventitious roots, "pseudo-neoplasms" on root-tips, and hypertrophy of the coleoptile in seedlings, and the stimulation of somatic growth in *Begonia*.

Havas believed he was dealing with a "phytohormone" comparable with the wound hormone, traumatin, yet concluded that colchicine is not a hormone but a mobilizer of the hormone already present in the plant. The hypertrophies produced on root-tips he (1939) thought analogous to crown-gall disease.

The contention of Dustin and his associates that colchicine inhibits tumor growth resulted in many studies designed especially to determine this point. Animal pathologists directed their attention to its effects on a number of different types of neoplasia in man and the lower animals, but no other type of plant overgrowth commonly referred to by botanists as tumors, such as the potato wart, club root, and nematode galls, has so far been investigated.

Brown (1939), one of the first investigators associated with experimental production of crown-gall, made a series of investigations to determine the therapeutic effect of colchicine on these bacterial overgrowths. She attempted to prevent crown-gall as well as to destroy it when fully formed. Eight species of plants were under observation, Paris daisy, French marigold, four

o'clock, *Bryophyllum*, *Kalanchoë*, *Nicotiana glauca*, kidney bean, and tomato. Brown concluded that colchicine does not prevent formation of the overgrowths caused by *B. tumefaciens* or indoleacetic acid.

Additional attempts to kill or prevent further development of fully grown crown-galls led to the conclusion that death of the galls was not due to the direct killing or inhibiting action of colchicine on the bacterial organisms but that the colchicine affected the growth substances in the plant.

Brown (1942) further studied the effects of acenaphthene, methylnaphthalene,  $\alpha$ -nitronaphthalene, 3,5-dibromopyridine, heptyl aldehyde and apiole. These substances were incorporated in a paste made of lanolin. Apiole induced dwarfing of the treated plant but no blackening of the tissue nor death;  $\alpha$ -methylnaphthalene (50 per cent and 100 per cent) inhibited growth, heptyl aldehyde, as well as  $\alpha$ -methylsalicylate used in full strength, caused death. The age of the tumor, Brown pointed out, affected the survival rate of the growth; young tumors were inhibited, old tumors were killed.

Dermen and Brown (1940a,b) studying the cytological effects of colchicine on plant tumors, found cellular changes associated with excessive polyploidy in the affected meristematic cells of the tumor. The effects induced by the colchicine were not immediate, for growth in controls and treated tumors continued for a week; then the treated tumors blackened and eventually died. The principal cytological change accompanying these morphological ones was multiploidy, which resulted in large nuclei in hypertrophied cells of the treated tissue. The size of the cells so produced had definite limits, the authors believed, beyond which death followed. Dermen and Brown suggested repeated colchicine injections in conjunction with irradiation as a therapeutic measure for cancer.

Solacolí, Constantinesco and Constantinesco (1939), who treated crown-galls on stems of *Pelargonium zonale* and *Ricinus communis* with colchicine, observed that a layer of meristem was formed between the tumor and the host; this new tissue became suberized and thus cut the metabolic exchange between plant and tumor so as to kill the new growth.

The effect of colchicine on animal tissue *in vivo* and *in vitro* has been reviewed by a number of workers and more recently by Levine (1945a,b). The reader is referred to these papers for details.

**Colchicine and X-rays.** Brues and Jackson (1937) studied the nuclear abnormalities induced by colchicine and other substances in a rat sarcoma, and suggested that the size of the dose determined the degree of aberrant cytological behavior. In a later paper, Brues, Marble and Jackson (1940) described the effects of the daily administration of colchicine on animal tumors and regenerating tissue. They believed that a narrow range of dosage exists that causes the characteristic effect upon cell division, and that this dosage can be injected daily without causing the death of the animal. The

belief that cells in mitosis are most susceptible to the effects of roentgen radiation led them to study the influence of x-rays on colchicinized tumors. Colchicine alone caused no regressions, though the tumors remained quiescent or retarded. As there was little difference between the tumors that were irradiated only and those given colchicine and irradiation, Brues and his associates concluded that colchicine has no effect on the response of these tumors to irradiation.

Guyer and Claus (1939), on the other hand, used 672 rats with Flexner-Jobling carcinoma in a series of experiments to test the combined effects of colchicine and x-rays on this tissue. They found that 0.1 mg. of colchicine per 100 g. of body weight administered subcutaneously coupled with irradiation of 3000r proved lethal to these animals in 2-3 weeks; 4500r given in three doses of 1500r each administered at intervals of two weeks or more were better tolerated, but smaller doses of 188r to 375r, frequently repeated, proved more effective than the larger doses. Guyer and Claus believed that a far greater lethal effect was produced in their experiments by the combined effects of colchicine and x-rays than by either one alone. In studying the combined effects of colchicine and x-rays on the Flexner-Jobling tumor *in vivo*, 91 rats were used. These were divided into 3 groups: 32 were treated with colchicine and x-rays, 29 with x-rays, and 30 with colchicine. The x-rays were given in doses of 188r twice weekly, beginning 16 days after implantation, when the tumors had attained a size of 1-1.5 cm., and 15 hours after the colchicine had been injected. At the end of 6 weeks in the group that received both x-rays and colchicine a large number of animals were healed; few deaths were recorded. Guyer and Claus concluded that x-rays are definitely more lethal to fragments of cancer tissue from colchicine-treated animals than to comparable pieces of untreated animals, as shown by the infrequency of takes after transplantation. When colchicine was administered to rats bearing actively growing tumors 15-18 hours before irradiation, x-rays retarded or completely inhibited tumor growth. Hirshfeld, Tennant and Oughterson (1940) studied the combined influence of colchicine and radiation on a transplantable mammary mouse carcinoma, and concluded that colchicine did not strikingly increase the destructive effects of x-rays, nor did it have any effect on the regression of spontaneous tumors in strain A mice.

Seed, Slaughter and Limarzi (1940) investigated the effect of colchicine combined with x-rays on advanced carcinomas in man. The 4 cases reported consisted of 2 breast adenocarcinomas, 1 rectal tumor, and one unclassified mass in the neck of a male. Two of the subjects died of colchicine poisoning and the others of their tumors.

**Acenaphthene and Other Substances.** The effect of tryptaflavine, sodium cacodylate, and colchicine on pathological and normal tissues stimu-

lated interest in the search for other substances which would induce similar changes. Dustin, Lits, Brues, Brown, and others have studied a number of substances with this point in view. Schmuk (1938) and later in association with Gusseva (1939) showed that acenaphthene, like colchicine, could induce polyploidy. The assumption that a certain relationship existed between polyploidizing substances and the carcinogenes led Schmuk and Gusseva to test many of these substances. The carcinogenes were dissolved in ether and poured over filter paper. When the ether evaporated, grains of corn, wheat, and barley were placed on the paper and water was added for germination. Schmuk found that wheat and barley seeds were polyploidized by acenaphthene, acenaphthylene, chloracenaphthene, bromacenaphthene,  $\alpha$ -chlornaphthalin,  $\alpha$ -bromonaphthalene,  $\alpha$ -iodonaphthalene,  $\alpha$ -dibromobenzol, methylnaphthalaether, 3,5-dibromopyridin, ethylnaphthoat,  $\alpha$ -nitronaphthalin. Germinating legume seeds did not become polyploid but were resistant to the effects of acenaphthene.

Kostoff (1938a) followed Schmuk with studies on germinating seeds of wheat, rye, oats, barley, maize, rice, *Festuca*, and *Lolium*. The seeds were covered with crystals of acenaphthene for 4–9 days. Legumes (*Vicia*, *Erodium*, *Lothyrus*, *Medicago*) reacted slowly after an exposure of 6–12 days, while *Compositae* responded in 4–8 days. Kostoff showed that mitoses proceeded abnormally, forming polyploid nuclei. The chromosomes were spread in the cytoplasm, frequently giving rise to multinucleate cells. Floral buds of nine species of *Nicotiana* treated with crystals of acenaphthene produced abnormal microspores and abortive pollen grains. The viable pollen grains had unequal numbers of chromosomes. Kostoff (1938b) induced chromosome doubling in species of *Triticum* and *Secale* by subjecting the seeds to a saturated solution of acenaphthene with excess of crystals. He pointed out that long exposures to large amounts of sublimated particles of acenaphthene may injure or even kill plant tissues. Nebel's (1938) results with saturated solutions of acenaphthene on *Tradescantia* gave no polyploidy. Acenaphthene, it must be remembered, is only very slightly soluble in water and the sublimated crystals, it seems, alone produce the reactions. Kostoff (1938c,d) later concluded that colchicine was toxic while acenaphthene did not appear to be. In a later report, Kostoff (1939) induced polyploidy in some series of cereals by subjecting them to pulp from disintegrating corms of *Colchicum autumnale*, which suggested the possibility of finding polyploid plants among the species growing in nature in association with *Colchicum*. Bates (1939) tested this theory and found that other plants growing among corms of the meadow saffron revealed no abnormalities. In nature, Bates believes the polyploid individuals are suppressed in competition with the normal seedlings or established vegetables.

Gavaudan, Gavaudan and Durand (1938) tested acenaphthene on ger-

minating wheat seedlings. They found themselves in accord with Kostoff in that acenaphthene prevents spindle formation. These investigators also tested the efficacy of diphenyl and naphthalene and their derivatives on dividing cells. While arrested mitoses were observed, some of the derivatives like diphenylmethane were toxic, Gavaudan (1941) tested (1,2,3,4,5-tetramethylbenzene) durene and found that it induced mitotic inhibition similar to acenaphthene. Gavaudan and Gavaudan (1939b) discovered that apiole inhibited cell division. They found that *Hordeum* seedlings were very susceptible to apiole and showed tetraploid and octoploid cells after the first 24 hours. After colchicine, the authors believed, apiole was the second known substance existing in a natural state capable of modifying nuclear and cell divisions and capable of inducing polyploidy.

Simonet and Guinochet (1939a) reported the production of polyploidy in flax seedlings by paradichlorobenzene. This substance produced morphological changes similar to those effected by colchicine and acenaphthene. Simonet and Igolen (1940) investigated the vapor of the oil of leaves of *Citrus nobilis* on flax and on barley seedlings. The roots of the latter were more sensitive than the flax and marked disturbances of cell and nuclear divisions were observed. Such stages as the anaphase and telophase were lacking and the cells became multinucleate. Methylene ester of methylanthranilic acid, the principal constituent of the oil of *C. nobilis*, produces similar reactions. Simonet and Guinochet (1939b) obtained effects with  $\alpha$ -chloronaphthalene and  $\alpha$ -bromonaphthalene which they believed comparable to those induced by colchicine. Simonet (1940) also claimed to have produced colchicine-like anomalies with 1,3,5-trinitro-m-xylene when barley and flax seedlings were tested. Shimamura (1939b) used sublimated acenaphthene on young flower buds of *Fritillaria* and observed abnormal nuclear division in pollen mother-cells. The pollen mother-cells divided into many cells, each containing small nuclei. Hukusima (1939) reported the production of polyploids in *Brassica alboglabra* with the aid of acenaphthene. The flowers were encased in small glass tubes, the walls of which were covered with crystals of acenaphthene. Favorski (1939) listed 12 chemicals among which were aurantia, tribromoaniline,  $\alpha$ - and  $\beta$ -naphthylamine, trinitrophenol, and tribromophenol, that induced mitotic changes similar to colchicine. Garrigues (1939) compared the effects of chloral and colchicine on the roots of *Vicia faba*. Chloral, he reported, did not induce swellings of the root but changed the structure of the resting nucleus. Chloral affected cells above the meristem interfering with the cells in the elongation zone. De Mol (1939) applied acenaphthene in paste form mixed with formalin, alcohol, or water to roots of gladiolus. The colchicine-formalin paste killed the roots, while the alcohol mixture injured them. De Mol concluded that acenaphthene is less effective than colchicine. Weichsel (1940) used auramin on *Vicia faba* and barley, and acenaphthene on *Soya*, luzerne, and corn. She reported changes similar

to those obtained by Schmuik and Kostoff on the grass seedlings with bromonaphthalene and bromoacenaphthalene. Fatalizade (1939), too, showed that crystals of acenaphthene acted on  $F_1$  seedlings of the cross *N. rustica*  $\times$  *N. paniculata* and produced polyploids.

**Colchicine in Cytology.** Many of the reports on the growth effects induced by colchicine are accompanied by cytological studies of the germ as well as the somatic cells. Many investigations on colchicine deal with the cytological changes per se. Dermen (1940) reviewed the literature on polyploidy as induced by colchicine and gave an adequate summary of the technique employed in the production of these aberrant chromosomal behaviors in plants and animals. Wellensiek (1939) gave a short digest of the use of colchicine in polyploidy as well as an historical account of the properties of the alkaloid. Györfy (1940a,b) studied the chromosome numbers of polyploids obtained by colchicine treatment. He also summarized the results obtained with colchicine treatment up to 1940. Here only those reports which have a bearing on the problem described below will be mentioned.

Nebel (1937) and Nebel and Ruttle (1938) studied the nuclear changes in the stamen hairs of *Tradescantia*. Gavaudan and Gavaudan (1937) treated plants with colchicine and reported the arrest of growth of plants with 0.001–0.005 per cent solution. They observed an increase in chromosome number. In a later paper (1938) they noted that the limit of increase in the number of chromosomes was determined only by the difficulties of nutrition. This they believed could be surmounted by cultivating plantules or polyploid cells in tissue culture. Gavaudan (1938) studied seedlings of *Vicia faba* which were immersed for two hours for three successive days in a 1:1000 solution of colchicine. These plants grew slowly and showed diverse monstrosities of stomata and leaf structures. Tetraploid and even octoploid cells with numerous nucleoli were observed. These changes were associated with interference with the normal karyokinetic process.

The roots of *Allium cepa* were studied by Gavaudan, Gavaudan and Pomriaskinsky-Kobozeff (1937) as affected by colchicine. They found that 0.1 g. to 0.2 g. of colchicine per 1000 ml. in water induced bulbous hypertrophies behind the meristem of the root-tips. They reported large numbers of abnormal mitotic figures 40 hours after treatment. Pseudonaphase stages were noted in which the chromosomes were vaguely arranged in a quadrilateral form (pseudotelophases) with the two chromosomal groups united by a bridge of chromosomal material.

Eigsti (1938, 1940a) using the smear method studied the effects of colchicine on the roots of the onion, and of radish and corn seedlings. He found that the cytological changes were determined by the concentration of the colchicine solution, the time of exposure, and the activity of the embryonic cells at the time of treatment. Eigsti (1940b) believes that chromosome breakage is higher in colchicine-treated material than in the untreated cells



of the same species. This, he infers, induces variation other than polyploid changes.

Levan (1938, 1939) made studies on the cytological effect of colchicine in mitoses of roots of *Allium fistulosum* and *A. cepa*. Levan, too, observed that the treated roots ceased to elongate, but formed swellings at the root-tip meristem which he described as tumors. The volume of the meristematic cells increases but no new cells are formed. Levan showed that the cells in treated roots transferred to water reverted to normal mitosis. In colchicized onion root-tips, he counted 128 and 256 chromosomes. Concentration as low as 0.0055 per cent colchicine caused disturbance of the spindle. The threshold value of colchicine on root mitoses of *A. cepa*, Levan believed, was reached with a 0.005–0.01 per cent solution after an exposure of four hours. Nebel (1937) found a 0.004 per cent solution of colchicine effective in plants, while Ludford (1936) showed that a solution of 0.00001 per cent is effective in animal tissue. Mangelot (1938a,b, 1939) studied the roots of onion (*Allium cepa*) and hyacinth (*Hyacinthus orientalis*), and of the seeds of lupine (*Lupinus albus*) grown in Knopf's solution to which 1:2000–1:3000 colchicine was added. He found that the roots remained alive after a long period in the mixture. He observed the *tumefaciens* effects of colchicine and ascribed this to a defect in the growth of the roots. The number of prophase stages was studied by Mangelot, who contended that the number of cells in this stage did not vary up to 102 hours of exposure to colchicine, after which it decreased slowly, while the number of metaphases, anaphases, and telophases fell off rapidly to zero. Levine and Gelber (1943) showed that with a colchicine concentration of 0.01 per cent, the maximum number of metaphase stages in the root-tips of *Allium cepa* was reached after an exposure of 24 hours. Continued exposure to the same solution caused a general reduction in the number of metaphases until the number reached in the 140th hour was smaller than that found in normal root-tips.

Shimamura (1939a) investigated the effects of the alkaloid, colchicine on the roots and seedlings of *Allium cepa*, *Lycopersicum esculentum*, and *L. pimpinellifolium*. He exposed the roots of the onion to a 0.4 per cent solution for two hours, after which they were placed in running water for one hour, and then fixed at varying intervals. Shimamura described in detail the chromosome behavior in the colchicine-treated onion root-tips. He believed that colchicine interfered with the mechanism that pulls the chromatids apart. In the absence of the spindle fibers Shimamura described an orientation of the chromosome material about a degenerate spindle substance. The tomato seedlings treated with colchicine produced tetraploid and myxoploid plants. In the roots of these seedlings aneuploidy was seen. Duhamet (1939) attempted to establish the colchicine concentration which would be most capable of producing a reaction in the roots of the white lupine grown *in vitro* and attempted to induce a diminution or suppression of these effects.

He observed that colchicine in concentration  $10^{-4}$  inhibited completely growth of isolated roots in 10–12 days. The addition of heteroauxine in concentration  $10^{-12}$  to this solution of colchicine interfered with the growth block induced by colchicine and was followed by a return to normal division. Levine and Lein (1941) studied the effects of various growth substances, such as vitamin B<sub>1</sub>, indoleacetic acid, and colchicine on the number and length of roots of *Allium cepa* grown in water in which these substances were used singly or in combination. Colchicine in  $10^{-3}$  solution inhibited root growth; when followed by exposure to a  $10^{-8}$  solution of indoleacetic acid, stimulation of both the formation of new roots and the linear growth of roots occurred.

**Irradiation with X-rays.** It has been now generally conceded that x-rays and the beta and gamma rays of radium are valuable adjuncts to surgery if not self-sufficient agents in the effective treatment of neoplastic diseases of man. Many roentgenologists believe that the efficacy of these rays lies in their destructive action on chromosomes. The resting stages have been considered resistant. However, there are two principal groups of investigators whose studies primarily dealt with these highly important problems. Strangeways and his associates Oakly and Hopwood observed that irradiated tissue culture showed a decrease in the number of dividing cells. They observed that this decrease was due temporarily to an inhibition of the onset of mitoses. These views were supported by Kemp and Juel. On the other hand, Mottram, Richards, Grasnich, Holthusen, Alberti and Politzer and many others contended that cells are most sensitive to irradiation while in the process of mitosis. Love's (1931) studies on choroid and sclerotic tissues of embryo chicks of 8–9 days attempt to analyze the effects of x-rays on dividing cells. He studied the percentage of survival of dividing cells immediately after irradiation. He concludes that the reduction in the number of cells in mitosis after irradiation is due to an inhibition of some factor of those cells which normally would have entered mitosis during the period of irradiation. He states that the radio-sensitivity of a cell is a function of its displacement from maturity. When the displacement of a cell from its maturity is less than 100 minutes, the radio-sensitivity is constant and independent of displacement. When the displacement of a cell from its maturity is greater than three hours, its radio-sensitivity decreases. Studies on the effects of irradiation on chromosomes of animals and plants are too numerous to be included here. The recent literature dealing with the application of irradiation to onion root-tips is briefly outlined below.

Nichols (1941), working with Sax, investigated the chromosomes of non-irradiated root-tips of onion seedlings. He reports that chromosome aberrations are frequent in very young seedlings, while in older ones few chromosome abnormalities are found. Nichols believes that cells with chromosome aberrations are eliminated by differential survival of the normal and ab-

normal cells. Marshak and Hudson (1937) used the onion seedling root-tips as a biological method of measuring roentgen ray dosage. They believe that the biological response per roentgen (r) is independent of wave length over the region studied. They used small doses, 40–346r. Marquardt (1938) studied the effects of soft rays on root-tips of *Scilla campanulata* and on pollen mitosis in *Bellevalia romana*. He describes two kinds of effects which he calls primary and secondary. The first effect occurs in such nuclei as are found, at the time of irradiation, in mitosis or about to enter that state. The primary effects are described as clumping and fragmentation of chromosomes, lack of spindle formation, and indefiniteness of division polarity. The period following the primary effects is a mitosis-free interim after which the secondary effects become apparent. In the pollen studies there was no mitosis-free interim. The secondary effects bring about chromosome injuries, fragmentations and restitution processes, lateral chromatid translocations, ring-forming injuries, and inversion forms. Villars (1940) studied the effects of x-irradiation on colchicine-treated roots of seedlings of *Pisum sativum* and *Allium cepa*. These were placed in a solution of 1:2000 colchicine and irradiated after 40, 48, 96, and 120 hours of immersion. Their treatment had no effect on stages up to and including the prophase. In the following stage, the chromosomes agglutinated and fused into one mass, and spindle formation was inhibited.

Sax (1941) studied the effects of x-irradiation on the roots of *Allium cepa*. While the primary purpose was to describe the chromosomal changes induced by the x-rays, an exposure to 0.1 per cent colchicine for 24 hours was applied to facilitate this study. Aberration frequency was based on the number of chromosomal abnormalities per 100 cells counted. Sax describes primary and secondary effects produced by x-rays which are in accord with Marquardt's observations. Sax does not differentiate between the effects induced by colchicine and those by x-rays. He shows that high x-ray doses suppress nuclear division for from one to two days while low x-ray doses retard nuclear activity and the chromosome clumping persists for several days. The primary effects are evident on the metaphases, while the secondary effect involves the production of chromosomal aberrations which consist of chromosome breaks, usually followed by chromosome union to produce rings, dicentrics, inversion, translocations, and interstitial deletions. The secondary x-ray effects, Sax believes, persist for several cell generations, but are soon eliminated and cells with normal or balanced genomes survive. Sax used doses of x-rays from 150r to 600r. Larger doses, such as 1500–5000r, were used on seedlings of ornamental plants; the highest dosage killed or retarded the seedlings of most species studied.

**The Function of Colchicine in Tumor Therapy.** It has been shown that colchicine administered or applied in small doses to animals or plants has a retarding effect on mitosis in the cells of either growing vegetative or

germinal tissue. In animals, the metaphases begin to accumulate 2-3 hours after the colchicine is given, reach a maximum number in 10-15 hours, and then gradually return to normal. In cold-blooded species, the accumulation of these mitotic figures is much slower, and lasts 5-7 days. In the roots of onions the metaphases reach a maximum number at 24 hours and then slowly decline, in spite of the continued application of the drug, to a stage where the divisions are fewer than in normal, untreated roots. The reconstructed nuclei after the treatment frequently form polyploid giant cells which persist or are eliminated.

In malignant animal growths colchicine emphasizes the division phase. Many of the chromosomal aberrations found in malignant cells (Levine 1931) are analogous to those induced by colchicine. The evidence that colchicine increases these stages in the tumor cell cycle has been well established. The young peripheral cells, apparently diploid, become arrested in division and present hyperchromatic stages typical of the older parts of the tumor. These considerations suggest the use of colchicine in cancer therapy. However, some cells in the animal tumors return to the status of young active cells, which leaves the tumor capable of continued growth. The attempt to destroy these cells by additional colchicine raises the colchicine level to the lethal point and so causes death of the animal.

The application of x-rays to tumor tissue after treatment with colchicine seems to be indicated. The colchicine keeps the active peripheral cells of a tumor in the metaphase stage so that a much larger number of cells in division, a vulnerable stage, are exposed to the lethal effect of x-rays.

The results so far presented, however, have been inconclusive. Some investigators have found that colchicine alone causes complete regression of lymphoid tumors; others have seen some improvements in animals with carcinomas or sarcomas after colchicine and x-rays combined over comparable neoplasms treated only with x-rays.

Tumors induced on plants by bacteria or chemical means were destroyed by colchicine alone. The self-limiting nature of these tumor-like growths, however, precludes any comparison between the effects of colchicine on animal tumors and on the crown-gall disease of plants. However, in some cases, the plant overgrowths appear to die sooner after colchicine treatment than when left to complete their life cycle.

It thus appears that a study of the combined effects of colchicine and x-rays on a simple fundamental tissue, meristematic in nature and responsive to both agents, would clarify the interpretation of the results obtained from them. It was believed that such a study would serve as a forerunner of an investigation on the effects of these agents on animal tumors of a cytogenetic homogeneity.

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# INDEX TO AMERICAN BOTANICAL LITERATURE

## PLANT TAXONOMY AND FLORISTICS

(exclusive of fungi)

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## INDEX TO VOLUME 72

New names and new combinations are indicated by **bold face** type

- Absidia orchidis*, 166; *ramosus*, 166  
*Acacia modesta*, 399  
 Acenaphthene, effect of on plant tissue, 567-570  
*Acer pseudoplatanus*, 151  
*Achlya flagellata*, 48, 51  
*Achorion schoenleinii*, 171  
*Achras balata*, 554; *calcicola*, 561; *chicle*, 561; *duplicata*, 554, 555; *sideroxylon*, 556; *zapota*, 551, 560; *zapotilla*, 551, 560  
*Achyranthus aspera*, 219  
*Acrostichum alpinum* 404; *maranteae*, 419; *septentrionale*, 416; *thelypteris*, 408; *vellea*, 419  
 Adanson, 52, 60-62  
*Adiantum capillus-veneris*, 402, 421; *caudatum*, 403, 421; *pedatum*, 402, 421, 497, 501; *venustum*, 421, 422  
*Aecidium desmitum*, 206; ***entebbense***, 221; *evansii*, 221; *phyllanthi*, 207, 221; *tubulosum*, 213; *vanderystianum*, 222; *vernoniae-podocoma*, 222  
*Aerobacter aerogenes*, 158, 161  
*Agraulis brevifolia*, 544  
*Agrostis*, a new section *Microphyllae* in, 541; *alopecuroides*, 544; *ampla*, 542-544, 546, 547; ***f. monolepis***, 547; *californica*, 542, 544; *exarata*, 541, 542, 544, 546; var. *ampla*, 542; var. *californica*, 542; var. *monolepis*, 541, 546; var. *pacifica*, 542; *hendersonii*, 541, 547; *inflata*, 543, 544, 546; ***kennedyana***, 543, 544, 547; *microphylla*, 543, 544, 546; var. *hendersonii*, 543, 544, 547; var. *intermedia*, 543, 544, 547; *rossae*, 542  
*Aira hawaiiensis*, 23; *f. depauperata*, 23; *f. haleakalensis*, 23; *praecox*, 23  
*Albizia grandibracteata*, 215; *lebbek*, 216; *procera*, 216  
*Alcaligenes fecalis*, 158, 161, 163  
*Alcornea cordifolia*, 205  
*Alectoria chalybeiformis*, 163  
*Allium cepa*, 570-573; *flatulosum*, 571  
*Amblystegiella confervoides*, 516; *subtilis*, 516  
*Amblystegium juratzkanum*, 516; *serpens*, 516; *varium*, 516  
 American botanical literature, index to, 114, 224, 335, 427, 483, 575  
*Amphilophis insculpta*, 209  
 Anatomy of peach and cherry phloem, 137  
*Andreaea rothia*, 511  
 ANDREWS, HENRY N., Cytoplasmic hybrids in *Penicillium notatum*, 361  
*Andropogon dummeri*, 209  
***Anglopora hansfordii***, 206  
*Anisoplidium ectocarpii*, 47  
*Anogramma leptophylla*, 402  
*Anomodon attenuatus*, 515; *minor*, 515; *rostratus*, 515; *rugelii*, 515; *tristis*, 515; *viticulosus*, 515  
 Antibacterial activity of fungi, 163  
 Antibiotic activity of lichens, 157  
*Antidesma venosa*, 207  
*Arctophyllum aristatum*, 299; *capitatum*, 299; *thymifolium*, 299  
*Aristolochia reticulata*, 270; *serpentaria*, 270  
*Armillaria mellea*, 169  
*Artemisia maritima*, 422  
*Arundinella nepalensis*, 218  
*Ashbya gossypii*, 166  
*Aspidium angulare*, 412; *aristatum*, 413; *bakerianum*, 412; *brunonianum*, 407; *caryotideum*, 413; *drenatum*, 413; *filix-mas*, 405; *fimbriatum*, 415; *goggilodus*, 22; *gongylodes*, 22; *luctuosum*, 412; *marginatum*, 406; *rufobarbatum*, 412; *squarrosum*, 412; *tsus-simense*, 412; *varians*, 417  
*Asplenium acrostichoides*, 414; *adiantum-nigrum*, 417, 420; *alternans*, 417; *oeterrach*, 418; *filix-femina* var. *attenuatum*, 415; var. *dentigerum*, 415; var. *polysporum*, 415; var. *retusum*, 415; *fimbriatum*, 415; *fontanum*, 402, 417; *latifolium*, 426; *mackinnoni*, 414; *maximum*, 426; *mcdonelli*, 414; *pekinense*, 417; *polypodioides*, 415; *rupicola*, 414; *rutamuraria*, 402, 416; *sarelitii*, 417; *saulitii*, 417; var. *pekinense*, 417; *schimperii*, 415; *septentrionale*, 402, 416; *squamigerum*, 416; *tenellum*, 414; *thelypteroides*, 414; *trichomanes*, 402, 416; *varians*, 417; *viride*, 402, 416  
*Athyrium acrostichoides*, 402, 414; *crenatum*, 413, 416; var. *glabratum*, 416; *filix-femina*, 402, 414, 415; var. *dentigerum*, 411, 415; var. *retusum*, 415; *fimbriatum*, 415; *japonicum*, 415; *mackinnoni*, 414; *maximum*, 426; *mcdonelli*, 414, 416; *nigripes*, 414; *pectinatum*, 414; *rupicola*, 414; *schimperii*, 415; *setiferum*, 401, 414; *thelypteroides*, 414

- Atrichum angustatum*, 519; var. *plurimellatum*, 519; *macmillani*, 519; *undulatum*, 519  
*Aulaecomnium heterostichum*, 513; *palustre*, 514  
*Bacillus cereus*, 158; *mycoides*, 158, 161; *subtilis*, 158-164  
*Bacterium tumefaciens*, 565, 566  
*Baeomyces aeruginosa*, 163; *placophyllus*, 163; *roseus*, 163  
BALDWIN, J. T., JR., Chromosomes of Cruciferae—II. Cytogeography of *Leavenworthia*, 367  
*Barbilophozia barbata*, 508, 509  
*Barbula unguiculata*, 512  
BARRETT, MARY F., *Ficus altissima*, 394  
*Bartramia pomiformis*, 514  
*Bassia albenscens*, 559  
*Bauhinia fassoglensis*, 208  
BETLE, ALAN A., A new section *Microphyllae* in *Agrostis*, 541  
*Bellevalia romana*, 573  
BENTLEY, NANCY J., Glandular leaf hairs of oriental tobacco, 345  
*Betula utilis*, 399  
*Blakea alternifolia*, 390; *andreaana*, 387; *bracteata*, 386; *brunnea*, 387; *calycosa*, 386; *calyptrata*, 388; var. *latior*, 388; *clausifolia*, 387; *cuatrecasii*, 387; *florifera*, 391; *glandulosa*, 386; *intercepta*, 387; *paleacea*, 389, 390; *pilosa*, 391; *platypoda*, 390; *podagrica*, 388; *pyxidanthus*, 388; *stellaris*, 390; *subconnata*, 388, 390; var. *obtusa*, 388; *venosa*, 389, 390  
*Blechnum radicans*, 418  
*Borreria laevis*, 300; *ocymoides*, 300  
Botanical literature, index to American, 114, 224, 335, 427, 483, 575  
*Bothriochloa decipiens*, 211  
*Botrychium*, the shoot of, interpreted as a series of dichotomies, 491; *boreale*, 491, 493; *chamaeconium*, 461; *dissectum*, 492, 494, 496, 500, 501; var. *obliquum*, 458, 492; *lanceolatum* var. *angustisegmentum*, 491, 494, 502; *lanuginosum*, 425, 492, 497, 498, 500; variations and origins of, 454-462; *lunaria*, 425, 492, 494, 497; var. *minganense*, 492; *matrigraefolium*, 493, 494, 498, 500; subsp. *typicum*, 492; *multifidum*, 492, 494, 498, 500, 502; subsp. *silaeifolium*, 492; subsp. *typicum*, 492, 496; *pumicola*, 492; *simplex*, 492; var. *compositum*, 492; var. *tenebrosum*, 492; *ternatum*, 502; *underwoodianum*, 492, 496; *virginianum*, 425, 454-462, 492, 496, 500, 502; subsp. *typicum*, 425; var. *lanuginosum*, 425  
*Brachiaria platynota*, 207  
*Brachythecium acutum*, 516; *digastrum*, 516; *oxycladon*, 516; *plumosum*, 517; *rivulare*, 517; *rutabulum*, 517; *salebrosus*, 517; *velutinum*, 508, 517  
*Brassica alboglabra*, 569  
*Brotherella delicatula*, 518; *recurvans*, 518  
*Bryhnia graminicolor*, 517; *novae-angliae*, 517  
Bryophytes of Shenandoah National Park, Virginia, 506  
*Bryum argenteum*, 513; *bimum*, 513; *caespitosum*, 513; *capillare*, 513  
*Bumelia conferta*, 558  
BURKHOLDER, PAUL R., Further studies on the antibiotic activity of lichens, 157  
*Calyptralla gracilis*, 473; *littoralis*, 473; *robusta*, 473; *tristis*, 473  
CAMP, W. H., *Vaccinium* hybrids and the development of new horticultural material, 1  
*Campbellosphaera obversa*, 131, 132, 134  
*Campyllum chrysophyllum*, 516; *hispidulum*, 516; *polygamum*, 516; *radicale*, 516  
Candolle, A. P. de, 52, 68, 69  
*Cardamine uniflora*, 367, 369  
*Cassia sieberiana*, 216  
*Cephaelis axillaris*, 300; *jamesonii*, 296, 300, 466, 470; *tomentosa*, 300  
*Cephalosporium acremonium*, 166  
*Cephalosia connivens*, 509  
*Cephalosziella hampeana*, 507, 509  
*Ceratodon purpureus*, 511  
*Ceratostomella fimbriata*, 166; *ips*, 166; *microspora*, 166; *minuta*, 166; *montium*, 166; *multiannulata*, 166; *obscura*, 166; *paradoxa*, 166; *penicillata*, 166; *piceaperda*, 166; *pilifera*, 166; *pini*, 166; *pseudotsugae*, 166; *radicicola*, 166; *rostrocylindrica*, 166, 179; *stenoceras*, 166; *ulmi*, 166, 179  
*Cerotelium delightonii*, 207; *dicentrae*, 207; *gossypii*, 206  
*Ceterach dalhousiae*, 417, 418, 420; *officinatum*, 402, 418, 420  
*Cetraria cucullata*, 161; *juniperina*, 163; *islandica*, 163; *nivalis*, 161; *oakesiana*, 163  
*Chalaropsis thielavioides*, 166  
*Chamberlainia acuminata*, 517; *biventrosa*, 508, 517; *cyrtophylla*, 517  
*Cheilanthes albomarginata*, 420; *dalhousiae*, 420; *farinosa*, 421; var. *albomarginata*, 420; var. *dalhousiae*, 420; *fragrans*, 420;

- nitidula*, 419; *persica*, 420; *pteridioides*, 402, 420; *subvillosa*, 419, 420; *szovitsii*, 420
- Chiloscyphus pallescens*, 508, 509; *polyanthus*, 508, 509; *rivularis*, 508, 509
- Chomelia barbellata*, 300
- Chromosomes of Cruciferae—II. Cytogeography of *Leavenworthia*, 567
- CHEYSLER, M. A., The shoot of *Botrychium* interpreted as a series of dichotomies, 491; The variations and origin of *Botrychium lanuginosum*, 454
- Chrysophyllum*, The North American species of, 191–204; *angustifolium*, 192, 201, 203; *argenteum*, 193; var. *sphaerocarpum*, 193; *bicolor*, 193, 197; *brachycalyx*, 200; *brachystylum*, 201; *brenesii*, 193, 196, 197; *caeruleum*, 193; *cainito*, 192, 198; var. *pomiferum*, 198; *claraense*, 192, 199; *eggersii*, 197; *glabrum*, 193; *gonavense*, 200; *heterochroum*, 201; *hirsutum*, 192, 198; *mexicanum*, 193, 202, 203; var. *politum*, 202, 203; var. *typicum*, 202; *miragoaneum*, 200; *montanum*, 203; *olivaceforme*, 192, 199–201, 203, 204; var. *pallescens*, 200; var. *picardae*, 200; var. *platyphyllum*, 200; var. *typicum*, 200; *pallescens*, 200; *panamense*, 193, 197; var. *macrophyllum*, 196, 197; *pauciflorum*, 193, 197; var. *krugii*, 195; var. *nervosum*, 195; *picardae*, 201; *platyphyllum*, 200; *tepicense*, 192, 198
- Chusquea scandens*, 470
- Cinchona corymbosa*, 468; *lanceolata*, 467; *officinalis*, 296, 301, 464; *pitayensis*, 296, 301; discovery and distribution of in Ecuador, 464–471; *pubescens*, 301, 305, 464, 468, 469
- Cirriphyllum boscii*, 517
- Citrus nobilis*, 569
- Cladonia alpestris*, 160; *amaurocraea*, 160; *apodocarpa*, 163; *atlantica*, 160; *basilaris*, 160; *borbonica*, 160, 163; *boryi*, 160; *brevis*, 160; *caespiticia*, 160, 162, 163; *capitata*, 160, 162, 163; *caroliniana*, 160; *chlorophaea*, 163; *clavulifera*, 163; *coniocraea*, 160, 164; *conista*, 163; *crisatella*, 160–164; *cryptochlorophaea*, 160, 164; *cyanipes*, 160; *deformis*, 160; *delicata*, 163; *fimbriata*, 160; *furcata*, 163; *glauca*, 160, 163; *gonecha*, 160; *gracilis* var. *choralia*, 160; var. *dilatata*, 163; var. *elongata*, 163; *grayi*, 160, 162–164; *incrassata*, 160; *macilentia*, 160; *mateocyatha*, 163; *meroclorophaea*, 160; *mittis*, 160, 161, 164; *nemoxyna*, 160; *ochrochlora*, 163; *papillaria*, 160; *pityrea*, 160; *pleurota*, 160, 161; *pyxidata*, 160; *rangiferina*, 163, 164; *robbsii*, 160; *santensis*, 163; *scabriuscula*, 163; *squamosa*, 160; var. *denticollis*, 163; *strepilis*, 160, 162, 163; *subcaryosa*, 163; *submitis*, 160; *subtenuis*, 160; *sybotica*, 160, 161; *turgida*, 163; *uncialis*, 160, 161; *verticillata*, 163
- Claudopus nidulans*, 172, 179
- Claviceps purpurea*, 163
- Clidemia crenulata*, 479; *epiphytica*, 479; *novemnervia*, 477; *panamensis*, 478; *petiolata*, 479; *ramiflora* var. *colombiana*, 478; *vallicola*, 477
- Climacium americanum*, 514; *dendroides*, 514; *kindbergii*, 514
- Clitocybe illudens*, 169, 170; *investiens*, 169; *tabescens*, 169
- Clostridium welchii*, 158, 163
- Cnidoscolus*, the genus in Mexico, 319; *aconitifolius*, 319–322, 331; *albidus*, 320; *angustidens*, 33, 326, 327; *armatus*, 320; *calyculatus*, 326; *chaya*, 321, 322; *chayamansa*, 32, 322; *elasticus*, 319, 320, 322, 323, 328; *hernandezii*, 323, 324, 333; *jurgensenii*, 324; *lebmannii*, 324; *macrandrus*, 324, 325; *multilobus*, 324, 325, 327, 329, 334; *orbiculatus*, 325, 326; *parviflorus*, 325, 326; *pringlei*, 326, 327; *rostratus*, 328; *souzae*, 328; *spinosus*, 320, 329, 330; *tenuilobus*, 319, 330; *tepiquensis*, 320, 323, 330–332; *tomentosus*, 332, 333; *tubulosus*, 32, 41, 320; *velutinus*, 325, 333, 334
- Coccocypselum condalia*, 302; *umbellatum*, 302
- Coffea arabica*, 302
- Colchicine, effect of on plant tissue, 563
- Collybia radicata*, 168; *velutipes*, 168
- Commelina vogelii*, 208
- Condaminea corymbosa*, 302
- Coniogramme affinis*, 419; *fraxinea*, 419
- Coniophora cerebella*, 172; *suffocata*, 172, 179
- Conocephalum conicum*, 511
- Conostegia cuatrecasii*, 473; *poepigii*, 474; *rubiginosa*, 473
- Coprinus radicans*, 168
- Cornus alba* var. *flaviramea*, 223; *asperifolia*, 223; *disciflora*, 223; var. *floccosa*, 223; f. *floccosa*, 223; *drummondii*, 223; f. *priceae*, 223; *florida*, 223; subsp. *urbiniana*, 223; var. *urbiniana*, 223; *priceae*, 223; *stolonifera*, 223; var. *flaviramea*, 223; f. *baileyi*, 223; f. *flaviramea*, 223; *urbiniana*, 223

- Corticium abeuns*, 170, 172, 180, 182-185, 187-189; *caeruleum*, 169; *confluens*, 169; *conigenum*, 172; *cremoricolor*, 168; *galactinum*, 169; *hydans*, 172, 180, 185, 186; *lividum*, 170, 172, 179; *roseum*, 169, 172; *salmonicolor*, 168
- Corynula pilosa*, 302
- Cotton, effect of on the germination of *Phycomyces* spores, 76
- COUZAT, LEON, "*Euphorbia chamaesyce*" in the United States, 312; History and nomenclature of the higher units of classification, 52
- CRONQUIST, ARTHUR, Studies in the Sapotaceae—I. The North American species of *Chrysophyllum*, 191; IV. The North American species of *Manilkara*, 550
- Crossospora antidesmiae-dioicae*, 207
- Cryptogramma brunnoniana*, 418; *crispa*, 418; *stelleri*, 402, 418
- CUMMINS, GEORGE B., Descriptions of tropical rusts—VII, 205
- Cyanococcus cuthbertii*, 5, 12
- Cyclophorus porosus*, 401, 424
- Cyclosorus gongylodes*, 22
- Cynoches chlorochilon*, 214
- Cymbopogon confertiflorus*, 209; *excavatus*, 209; *giganteus*, 209; *martini*, 209
- Cyrtomium caryotideum*, 403, 413
- Cystopteris fragilis*, 399, 402, 404; *montana*, 402, 404; *retusa*, 415
- Cytidia salicina*, 168
- Cytoplasmic hybrids in *Penicillium notatum*, 361
- Dactylina arctica*, 163
- Daedalia ambigua*, 168; *confragosa*, 168; *heteromorpha*, 172; *juniperina*, 172; *quercina*, 172; *unicolor*, 168
- DARROW, GEORGE M., *Vaccinium* hybrids and the development of new horticultural material, 1
- Datura stramonium*, 254
- Davallia pulchra*, 413
- DAVIDSON, ROSS W., A survey of some wood-destroying and other fungi for antibacterial activity, 165
- Dermatocarpon minutum*, 163
- Dermatophytes, 171, 178
- Deschampsia australis*, 23; *hawaiiensis*, 23; *f. depauperata*, 23; *f. haleakalensis*, 23
- Descriptions of tropical rusts—VII, 205
- Dicranella heteromalla*, 511; *varia*, 508, 511
- Dicrano-weisia crispula*, 508, 512
- Dicranum bonjeani*, 512; *flagellare*, 512; *fulvum*, 512; *fuscoseens*, 512; *montanum*, 512; *rugosum*, 512; *scoparium*, 512
- Dioclea reflexa*, 219
- Diplazium fraxineum*, 419; *japonicum*, 415; *maximium*, 401, 426; *polypodioides*, 415, 426; *squamigerum*, 413, 416
- Diphysium foliosum*, 519
- Diplococcus pneumoniae*, 158, 161
- Diplophyllum apiculatum*, 510
- Discovery and distribution of *Cinchona pitayensis* in Ecuador, 464
- Ditrichum lineare*, 508, 511; *pallidum*, 511; *pusillum*, 511
- Drosophila melanogaster*, 235
- Drummondia prorepens*, 514
- Dryopteris*, *Deschampsia*, *Portulaca*, *Lupinus*, *Fagara*, *Stenogyne*, and *Dubautia*. Hawaiian plant studies 12, 22
- Dryopteris africana*, 401, 409; *barbigera*, 407, 411; var. *falconeri*, 407; *blanfordii*, 405, 406; *brunnea*, 409, 426; *brunoniana*, 407, 411; *cochleata*, 406; var. *schimperiana*, 406; *crenata*, 407; *dentata*, 403, 409; *erubescens*, 408; *filix-mas*, 402, 405, 406; var. *odontoloma*, 405; *gongyloides*, 22, 23; *gongylodes*, 22, 23; *hexagonoptera*, 401, 411; *hirtipes*, 401; var. *atrata*, 408; *laterepens*, 400, 409, 426; *levingei*, 409; *linnaeana*, 402, 410, 411; *ludens*, 403; *macrocarpa*, 401, 406; *marginata*, 401, 405, 406; *moulmeinensis*, 408; *odontoloma*, 405; *paleacea*, 405; *parasitica*, 409; *penangiana*, 408; *phlegopteris*, 402, 410; *prolifera*, 401, 403, 409; *punctata*, 411; *ramosa*, 405, 406; *rampans*, 403, 408; *repens*, 401, 408; *robertiana*, 402, 410, 411; *rosthornii*, 404, 405; *schimperiana*, 401, 406; *serrato-dentata*, 406; *subpubescens*, 409; *thelypteris*, 402, 408
- Dubautia*, 22; *plantaginea*, 26-28; var. *angustifolia*, 26, 28, 29; var. *chamissonii*, 26, 30; var. *glandulosa*, 30; var. *paucicaulis*, 30; var. *strigosa*, 30; var. *typica*, 26, 30
- DWYER, JOHN D., The taxonomy of the genus *Sauvagesia* (Ochnaceae), 521
- Echinodonta tinctorum*, 169
- Ecuador, *Cinchona pitayensis* in, 464; Rubiaceae from, 295
- Effect of cotton on the germination of *Phycomyces* spores, 76
- Effect of colchicine and acenaphthene in combination with x-rays on plant tissue—I. Introduction, 563

- Elaeagnus utilis*, 302  
*Encalypta streptocarpa*, 512  
*Endoconidiophora adiposa*, 166; *caerulescens*, 166  
*Entodon brevisetis*, 517; *cladorrhizans*, 517; *seductrix*, 517  
*Epidermophyton inguinale*, 171, 178  
*Equisetum arvense*, 425; *debile*, 425, 426; *ramosissimum*, 425, 426  
*Escherichia coli*, 158, 161, 163, 165-189  
*Espeletia hartwigiana*, 466  
Estimates of the minimum numbers of genes differentiating several taxonomic categories in the genus *Solidago*, 235  
“*Euphorbia chamaesyce*” in the United States, 312  
*Euphorbia callitrichoides*, 317; *chamaesyce*, 312-317; var. *canescens*, 315; *humifusa*, 316; *mili*, 313; *portulacoides*, 317; *prostrata*, 312-317; *thymifolia*, 315  
*Eurhynchium hians*, 517; *rusciforme*, 517; *serrulatum*, 517; *strigosum*, 517; var. *praecox*, 517  
EVANS, ALEXANDER W., Further studies on the antibiotic activity of lichens, 157  
*Evernia vulpina*, 163  
*Ezidia glandulosa*, 168  
  
*Fagara*, 22; *dipetala* var. *geminicarpa*, 24; *mauiensis* var. *anceps* f. *petiolulata*, 25  
*Faramaea coerulescens*, 302; *maynensis*, 302; *oblongifolia*, 302  
FASSETT, NORMAN C., *Juniperus virginiana*, *J. horizontalis*, and *J. scopulorum*—III. Possible hybridization of *J. horizontalis* and *J. scopulorum*, 42; IV. Hybrid swarms of *J. virginiana* and *J. horizontalis*, 379; V. Taxonomic treatment, 480  
*Favolus canadensis*, 168  
Ferns of Kashmir, 399  
*Ficus altissima*, 394-398; var. *fergusonii*, 397, 398; var. *laccifera*, 394, 397; f. *laccifera*, 394; *bengalensis*, 394, 395, 397, 398; *capensis*, 207; *indica*, 394, 397; *laccifera*, 394, 396-398; *pcguensis*, 394, 397, 398; *varenga*, 394, 397, 398; *variegatus*, 207  
*Filix montana*, 404  
*Fissidens adiantoides*, 511; *cristatus*, 511; *minutulus*, 511; *osmundioides*, 511; *subbasilaris*, 511; *taxifolius*, 511; *viridulus*, 508  
*Fistulina hepatica*, 172  
*Flammula alnicola*, 172, 179  
*Fomes annosus*, 172, 180; *aplanatus*, 171, 172; *calkinsii*, 168; *clelandii*, 169; *conchatus*, 169; *connatus*, 168; *densus*, 168; *everhartii*, 168; *extensus*, 169; *ferruginosus*, 172; *fometarius*, 168; *fraxineus*, 168; *fraxinophilus*, 172, 173; *fulvus*, 169, 170; *geotropus*, 169; *igniarius*, 168; var. *laevigatus*, 168; var. *populinus*, 169; *juniperinus*, 173, 180, 187; *lobatus*, 169; *marmoratus*, 169; *meliae*, 173; *officinalis*, 173; *pini*, 173; var. *abietis*, 173; *pinicola*, 173; *pomaceus*, 169, 170; *ribis*, 173, 180-182, 187; *rimosus*, 168, 169; *robustus*, 168; var. *tsugina*, 168; *roseus*, 173; *scutellatus*, 169; *subroseus*, 173; *tenuis*, 173; *torulosus*, 168; *ulmarius*, 179; *ungulatus*, 173  
*Fontinalis novae-angliae*, 514  
*Frazinus excelsior*, 151  
*Frullania asagrayana*, 510; *brittoniae*, 510; *eboracensis*, 510; *riparia*, 510  
FULLING, EDMUND H., Thomas Jefferson. His interest in plant life as revealed in his writings—II, 248  
Further studies on the antibiotic activity of lichens, 157  
*Fusarium avenaceum*, 166  
  
*Galium aparine*, 303; *canescens*, 303; *pili-ferum*, 303; *tetraplazium*, 303  
*Ganoderma* sp., 173  
*Gastridium lendigerum*, 547  
*Gaylussacia brachycera*, 10  
Genus *Cnidoscolus* in Mexico: new species and critical notes, 319  
Genus *Jatropha* in America: principal intrageneric groups, 271  
*Gibberella saubinetii*, 166; *zeae*, 166  
Glandular leaf-hairs of oriental tobacco, 345  
GLEASON, H. A., On *Blakea* and *Topobea*, 385; Some Melastomaceae of Colombia, 472  
*Gomozia granadensis*, 303  
*Gomphosphaeria lacustris*, 246  
*Goniophlebium lachnopus*, 423; *micro-rhizoma*, 422; *argutum*, 423  
*Goniopteris lineata*, 408; *prolifera*, 409  
*Gonzalagunia cornifolia*, 303; *dependens*, 304; *runis*, 304; *soraria*, 304  
GOODWIN, RICHARD H., Estimates of the minimum numbers of genes differentiating several taxonomic categories in the genus *Solidago*, 235  
*Gossypium acuminatum*, 206  
*Grammitis vestita*, 418  
*Grimmia alpicola* var. *rivularis*, 512; *apocarpa*, 513; var. *conferta*, 513; var. *gracilis*, 513; *pilifera*, 513  
*Grossmannia serpens*, 166

- Guettarda hirsuta*, 304; *sabiceoides*, 304  
*Gymnocarpium dryopteris*, 410; *remotum*, 410; *robertianum*, 410, 411  
*Gymnogramma aurita* var. *levingei*, 409; *javanica*, 418; *leptophylla*, 402; *levingei*, 409; *totta*, 409; *vestita*, 418  
*Gymnopteris vestita*, 418  
  
*Hamelia patens*, 304; *pedicellata*, 304  
Hawaiian plant studies, 22  
*Hedwigia ciliata*, 514  
*Hemarthria uncinata*, 211  
*Hemidictyum ceterach*, 418  
*Hemidiodia ocimifolia*, 304  
*Hemionitis prolifera*, 409  
HERVEY, ANNETTE, A survey of some wood-destroying and other fungi for antibacterial activity, 165  
*Heterophyllum haldanianum*, 518  
*Hillia parasitica*, 304  
*Hirneola* sp., 173  
History and nomenclature of the higher units of classification, 52  
*Hoffmannia ecuatoriana*, 305; *sprucei*, 305  
*Homomallium adnatum*, 518  
*Hyacinthus orientalis*, 571  
*Hydnum abietis*, 173, 180, 186; *caput-ursi*, 174; *chrysocomum*, 168; *coralloides*, 169, 170; *erinaceus*, 169, 170; *ochraceum*, 168; *pulcherrimum*, 168; *scheidermayeri*, 174, 179; *septentrionale*, 174, 180, 184, 186  
*Hydrastis canadensis*, 270  
*Hygroamblystegium fluviatile*, 516; var. *ovatum*, 516; *irriguum*, 516; var. *spinifolium*, 516; *orthocladon*, 516  
*Hygrohypnum dilatatum*, 516; *eugyrium*, 516  
*Hylocomnium brevirostre*, 519; *splendens*, 519; *umbratum*, 508  
*Hymenochaete agglutinans*, 169; *corrugata*, 174, 179; *curtisii*, 169; *rubiginosa*, 169, 174, 179; *tabacina*, 174  
*Hyparrhenia rufa*, 209  
*Hypnum arcuatum*, 518; *cupressiforme*, 518; *curvifolium*, 518; *fertile*, 518; *imponeus*, 518; *molluscum*, 518; *pallenscens*, 508, 518; *reptile*, 518  
*Hypholoma sublateritium*, 174  
*Hypolepis punctata*, 411  
  
Index to American botanical literature, 114, 224, 335, 427, 483, 575  
*Indigofera arrecta*, 216  
Inheritance of orange and yellow flower color in *Nemesia strumosa*, 435  
*Inula acervata*, 221  
  
*Irpex cinnamomeus*, 174; *mollis*, 174, 180, 186, 187, 189  
*Isertia alba*, 305; *pittieri*, 305  
*Ithyphallus* sp., 174  
  
*Jamesoniella autumnalis*, 510  
*Jasminum pauciflorum*, 218  
*Jatropha*, The genus in America, 271; *acerifolia*, 292; *aconitifolia*, 319; *acuminata*, 274, 292; *alamani*, 33, 35, 288, 289, 292; *andrieuxii*, 276, 278, 283, 284, 292; *angustifolia*, 274, 292, 293; *antisiphilitica*, 292; *arizonica*, 292; *augusti*, 276-278, 292; *berlandieri*, 32, 276, 277, 292; *berterii*, 292; *bornmülleri*, 280, 292; *brachypoda*, 280, 281, 292; *breviloba*, 280, 292; *canescens*, 289, 292; *capensis*, 274; *cardiophylla*, 33, 288, 291, 292; *cathartica*, 32, 272, 277, 292; *catingae*, 291, 292; *cercidiphylla*, 292; *ciliata*, 35, 36, 41, 276-279, 288, 289, 292, 293; *cinerea*, 33, 36, 286-289, 292, 293; *clavuligera*, 280, 282, 293; *coccinea*, 293; *cordata*, 33, 35, 37, 272, 288, 290, 291, 293; *cuneata*, 36, 286, 287, 293; *cuneifolia*, 293; *curcas*, 33, 35, 271-273, 278, 283-285, 292-294; var. *rufa*, 272, 284; *decepiens*, 293; *dioica*, 36, 37, 41, 286, 290-293; var. *graminea*, 36, 39, 287; var. *sessiliflora*, 36, 37, 41, 287; *dissecta*, 280, 281, 293; *divaricata*, 273, 286, 293; *divergens*, 293; *diversifolia*, 274, 275, 293; *edulis*, 36, 37, 41, 292, 293; *elegans*, 293; *elliptica*, 280, 281, 293; *excisa*, 272, 280, 293; *flabellifolia*, 293; *flavovirens*, 280, 281, 293; *fremontiioides*, 285, 286, 293; *gaumeri*, 275, 285, 286, 293; *glauca*, 293; *glaucovirens*, 274, 275, 293; *gossypifolia*, 40, 273, 275, 278, 279, 281, 282, 293, 294; var. *elegans*, 32; *grandifrons*, 35, 41, 293; *grossidentata*, 276, 277, 293; *guaranitica*, 280, 293; *harmisiana*, 290, 293; *hastata*, 33, 273-275, 293; *hernandiaefolia*, 33, 286, 293, 294; *hernandifolia*, 273; *heterophylla*, 33, 41, 293; *hieronymi*, 276, 277, 293; *hippocastanifolia*, 281, 293; *hoffmanniae*, 35, 276, 277, 293; *humboldtiana*, 35, 41, 272, 277, 293, 294; *induta*, 280, 281, 293; *integerima*, 33, 272, 274, 275, 278, 292-294; *intercedens*, 281, 293; *intermedia*, 280, 293; *isabelli*, 280, 281, 292, 293; var. *antisiphilitica*, 280; *jacquini*, 293; *jurgensii*, 319, 324; *katharinae*, 280, 293; *lacey*, 293; *liebmannii*, 319, 324; *loeflingii*, 293; *longipedunculata*, 35, 276, 293; *luxurians*, 293; *macrantha*, 271,

- 275-277, 279, 293; *macrocarpa*, 276, 277, 279, 293; *macrorrhiza*, 279, 281, 292, 293; var. *septemfida*, 292; *malacophylla*, 287, 288, 290; *malmeana*, 281, 293; *martinsii*, 276, 293; *minor*, 275, 293; *mitis*, 293; *mollissima*, 279, 293, 294; *moluensis*, 33, 41, 275, 293; *multifida*, 32, 273, 276, 277, 293; *multiflora*, 276, 293; *multiloba*, 324; *mutabilis*, 276, 277, 293; *neopauciflora*, 37, 286, 287, 290, 293, 294; *nudicaulis*, 276, 277, 293; *octandra*, 41; *officinalis*, 293; *olivacea*, 32, 35, 41, 293; *opifera*, 293; *ortygae*, 286, 288, 290, 293; *pachypoda*, 276, 277, 279, 293; *palmata*, 39, 41; *palmatifolia*, 291, 293; *palustris*, 293; *panduraefolia*, 274, 275, 294; *papyrifera*, 276, 277, 294; *pauciflora*, 274, 275, 294; *paxii*, 274, 293, 294; *pedanti-partita*, 281, 282, 294; *peiranoi*, 280, 294; *peltata*, 34, 41, 276, 277, 294; *platani-folia*, 278, 290, 294; *platyphylla*, 32, 34, 286, 294; *podagrica*, 32, 34, 276, 277, 294; *pohliana*, 276, 277, 279, 294; *portoricensis*, 294; *prunifolia*, 274; *pseudocurcas*, 282, 284, 294; *punciculata*, 280, 294; *purpurea*, 280, 281, 294; *quinqueloba*, 40, 41; *ribifolia*, 280, 281, 294; *ricinifolia*, 276, 277, 279, 294; *rigidifolia*, 280, 294; *riogae*, 286, 288, 291, 294; *robertii*, 277, 294; *rufescens*, 287, 294; *spathulata*, 36, 37, 41, 290, 294; var. *genuina*, 37; var. *sessiliflora*, 33, 37; *standleyi*, 286, 288, 291, 294; *staphysagrifolia*, 294; *stigmatica*, 291, 294; *sympetalata*, 286, 287, 291, 294; *tacumbensis*, 281, 294; *tepiquensis*, 331; *thyr-santha*, 280, 281, 294; *transiens*, 280, 281, 294; *triloba*, 39-41; *tubulosa*, 40; var. *quinqueloba*, 40; var. *septemloba*, 40; *tupifolia*, 274, 275, 294; *unicostata*, 274; *variegata*, 274; *variifolia*, 274; *vernica*, 288, 291, 294; *villosa*, 294; *weberbaueri*, 35, 276, 277, 294; *wedeliana*, 276, 277, 279, 294; *yucatanensis*, 35, 41, 294
- Jatrophas* of Cervantes and of the Sessé and Mociño herbarium, 31
- Jaume-St. Hilaire, 52, 69-71
- Jefferson, Thomas, 248
- Jeffersonia*, 269; *binata*, 270; *diphylla*, 270
- Joosia pulcherrima*, 305
- Jubula pennsylvanica*, 510
- Juglans alba*, 252; *pecan*, 253; *paccan*, 253
- Juniperus communis* var. *depressa*, 43; *horizontalis*, 42, 43, 45, 46, 379-383, 480-482; *lucayana*, 482; *sabina* var. *procumbens*, 46; *scopulorum*, 42-46, 379-384, 480-482; var. *columnaris*, 480-482; var. *patens*, 44-46, 480-482; *silicicola*, 482; *virginiana*, 45, 46, 379-384, 480-482; var. *ambigens*, 380-383, 480-482; var. *crebra*, 480-482
- Juniperus virginiana*, *J. horizontalis*, and *J. scopulorum*—III. Possible hybridization of *J. horizontalis* and *J. scopulorum*, 42; IV. Hybrid swarms of *J. virginiana* and *J. horizontalis*, 379; V. Taxonomic treatment, 480
- Jussieu, Antoine Laurent de, 64, 65; Bernard de, 65
- KARLING, JOHN S., *Rhizidiomyces hirsutus* sp. nov., a hairy anisochytrid from Brazil, 47
- Kashmir, The ferns of, 399
- Kuehneola desmum*, 206; *gossypii*, 206
- Lactobacillus casei*, 158, 163
- Ladenbergia macrocarpa*, 305; *magnifolia*, 305
- Lamarck, 52, 63, 64
- Lastrea atrata*, 408; *barbigera*, 407; *brunoniana*, 407; *crenata*, 407; *falconeri*, 407; *filix-mas* var. *elongata*, 406; var. *odontoloma*, 406; var. *parallelogramma*, 404; var. *schimperiana*, 406; var. *serrato-dentata*, 406; *hirtipes*, 408; *odontoloma*, 405; *thelypteris*, 408
- Leavenworthia*, cytogeography of, 367; *aurca*, 367-369, 373-377; *michauxii*, 367, 369; *stylosa*, 368-370, 372-377; *torulosa*, 367-373, 375, 377; *uniflora*, 367, 368, 370, 373, 375-377
- Leitgebia imthurnia*, 528
- Lejeunea cavifolia*, 511; *patens*, 511
- Lentinus lepidius*, 169, 170; *tigrinus*, 168; *villosa*, 168
- Lenzites betulina*, 168; *trabea*, 168-170; *saepiaria*, 170, 174
- Lepiota naucina*, 174, 180, 186, 187
- Lepisorus loriformis*, 423
- Leptodictyum trichopodium* var. *kochii*, 516
- Leptogramme totta*, 409
- Leptostegia lucida*, 421
- Leskea obscura*, 515; *polycarpa*, 515
- Leucobryum albidum*, 512; *glaucum*, 512
- Leucodon brachypus*, 514; *julaceus* f. *flagelliferus*, 514; *sciuroides*, 514; *trichomitrium*, 515
- Leucolejeunea clypeata*, 511
- Leucostegia pulchra*, 401, 413
- LEVINE, MICHAEL, The effect of colchicine and acenaphthene in combination with

- x-rays on plant tissue—I. Introduction, 563
- Lichens, further studies on antibiotic activity of, 157
- LINDEGREN, CARL C., Cytoplasmic hybrids in *Penicillium notatum*, 361
- Lindley, 52, 70
- Linnaeus, 52, 54–63
- Lippia asperifolia*, 221; *berlandieri*, 222
- Lobaria pulmonaria*, 163
- Lophocolea bidentata*, 509; *heterophylla*, 509; *minor*, 507, 509
- Loureira cuneifolia*, 37; *glandulosa*, 290
- LUNDELL, CYRUS LONGWORTH, The genus *Cnidioscolus* in Mexico; new species and critical notes, 319
- Lupinus*, 22; *albus*, 571; var. *termis*, 24
- Lycoperdon gemmatum*, 169; *pyriforme*, 169
- Lycopersicum esculentum*, 571; *pimpinellifolium*, 571
- Lycopodium sanguinolentum*, 426; *selago*, 426; f. *angustum*, 426
- Lygodium japonicum*, 424
- MA, ROBERTA, A survey of some wood-deströying and other fungi for antibacterial activity, 165
- Macrocnemum sprucei*, 306
- Manetta echitidea*, 306; *evenia*, 306; *flexilis*, 306; *pichinchensis*, 306; *racemosa*, 306; *recurva*, 306; *skutchii*, 306; *trianae*, 306
- Manihot aesculifolia*, 39; *fetida*, 32, 34, 40; *palmata*, 39
- Manilkara*, The North American species of, 550; *albescens*, 553, 558; *bidentata*, 551, 552, 554; *breviloba*, 560; *calciolata*, 561; var. *columbiana*, 561; *calderonii*, 560; *chicle*, 553, 561; *consattii*, 560; *darienensis*, 553; *duplicata*, 554; *emarginata*, 551, 553, 556, 558; subsp. *haitiensis*, 558; subsp. *jaimiqui*, 557–559; subsp. *typica*, 557; subsp. *wrightiana*, 557; *excisa*, 552, 555; *gaumeri*, 560; *gonavensis*, 553, 562; *grisebachii*, 557, 558; *howardii*, 557; *jaimiqui*, 557; *mayarensis*, 553, 558, 559; *meridionalis*, 551, 553, 560; var. *caribbensis*, 560; var. *meridionalis*, 560; *nitida*, 553; *pleeana*, 552, 554; *riedleana*, 553; *rojasi*, 560; *sideroxylon*, 553, 555, 556; *sapodilla*, 552; *spectabilis*, 552, 555; *staminodella*, 551, 553, 560; *striata*, 560; *tabogaensis*, 560; *wrightiana*, 557; *zapotilla*, 551, 553, 556, 560
- Manisurus altissima*, 211
- Marsilia erosa*, 425; *minuta*, 425; *natans*, 425
- Marsupella emarginata*, 510
- McVAUGH, ROGERS, The genus *Jatropha* in America: principal intrageneric groups, 271; The *Jatrophas* of Cervantes and of the Sessé and Mocino herbarium, 31
- Melandryum viscosum*, 349
- Melastomaceae of Colombia, 472
- Melinis tenuissima*, 206
- Mentha piperita*, 350
- Merrillosphaera carteri*, 132
- Merulius confluentis*, 169; *niveus*, 168; *tremellosus*, 168
- Metzgeria conjugata*, 511; *crassipilis*, 511
- METZNER, JEROME, A morphological and cytological study of a new form of *Volvox*—I, 86; II, 121
- Miconia axinawides*, 476; *barbinervis*, 477; *blakeaeifolia*, 475; *calcarata*, 474; *centronioides*, 475, 476; *clavistyla*, 477; *compacta*, 477; *dolichorrhyncha*, 477; *gracilis*, 476; *lanata*, 477; *marginata*, 476; *megalantha*, 476; *pilgeriana*, 477; *platypoda*, 476; *ruicalyx*, 477; *semota*, 477; *stelligera*, 477; *stipitata*, 476; *transversa*, 475
- Microlepidozia sylvatica*, 509
- Microlepis wilfordii*, 413
- Microsporum canis*, 178; *felineum*, 171; *gypseum*, 171
- Mimena holwayi*, 216
- Morchella esculenta*, 166, 168
- Morphological and cytological study of a new form of *Volvox*—I, 86; II, 121
- Mozinna canescens*, 290; *cordata*, 290; *sessiliflora*, 37; *spathulata*, 36, 37, 282, 285; var. *sessiliflora*, 37
- Mucuna urens*, 219
- Mimusops albescens*, 559; *azulensis*, 559; *balata*, 554; var. *domingensis*, 553; var. *sieberi*, 553; *bidentata*, 553, 554; *camagueyensis*, 557; *darienensis*, 553; *duplicata*, 554; *excisa*, 555; *floridana*, 557; *gonavensis*, 561; *grisebachii*, 557; *jaimiqui*, 557; *jamaicensis*, 556; *kaukii*, 550; *mayarensis*, 558; *nitida*, 553; *parviflora*, 557; *pleeana*, 554; *riedleana*, 553; *sideroxylon*, 556; *sieberi*, 553, 557; *wrighteana*, 557
- Mniobryum albicans*, 513
- Mnium affine*, 513; *cuspidatum*, 513; *hornum*, 513; *marginatum*, 513; *orthorrhynchum*, 508, 513; *punctatum*, 513; *stellare*, 513
- Murica albescens*, 559; *eyerdamii*, 559



- Necker, 52, 66  
*Neckera pennata*, 515  
*Nemesia compacta*, 436; *grandiflora*, 436; *strumosa*, 435-452; inheritance of orange and yellow flower color in, 435; *strumosa suttoni*, 436; *versicolor*, 436  
*Nephrodium aristatum*, 413; var. *affine*, 413; *barbigerum*, 407; *blanfordii*, 405; *brunonianum*, 407; *costatum*, 408; *falconeri*, 407; *filix-mas*, 405; var. *elongatum*, 406; var. *fibrillosum*, 404; var. *marginatum*, 406; var. *normale*, 405; var. *schimperianum*, 406; *hirtipes*, 408; *kingii*, 406; *marginatum*, 406; *molle*, 409; *odontoloma*, 405; *prolixum*, 408; *rampans*, 405; *remotum*, 405; *repens*, 408; *rigidum*, 405; *rosthornii*, 404; *schimperianum*, 406; *serrato-dentatum*, 406  
*Nephromopsis ciliaris*, 163  
*Nertera depressa*, 303  
*Neurospora crassa*, 166; *sitophila*, 166  
New combinations in *Cornus*, 223  
New section *Microphyllae* in *Agrostis*, 541  
*Nicotiana*, 345-360; *alata*, 438; *glauca*, 566; *langsдорffii*, 438  
*Niphobolus fissus*, 424; *porosus*, 424  
*Notholaena marantae*, 401, 402, 419; *persica*, 420; *vellea*, 401, 402, 419  
*Nowellia curvifolia*, 509  
  
*Odontoschisma denudatum*, 509  
*Olea cuspidata*, 399  
*Omphalia campanella*, 174  
On *Blakea* and *Topobea*, 385  
*Onychium contiguum*, 421; *japonicum* var. *lucidum*, 421; var. *multisectum*, 421; *lucidum*, 421  
*Ophiobolus oryzinus*, 166  
*Ophioglossum engelmanni*, 497, 501; *fibrosum*, 498; *japonicum*, 424; *vulgatum*, 425  
*Ophiostoma catonianum*, 166  
*Orthotrichum ohioense*, 514; *speciosum*, 514  
*Osmunda claytoniana*, 402, 411, 424; *lunaria*, 425; *regalis*, 402; *virginiana*, 425  
*Ossaea resinosa*, 478  
*Oxalis violacea*, 371  
*Oxycoccus macrocarpus*, 1  
  
*Palicourea angustifolia*, 306; *balnearia*, 307; *calantha*, 307; *caldasiana*, 307; *calothyrsus*, 307; *chimboracensis*, 307; *crocea*, 307; *egena*, 307; *flavescens*, 307; *gutianensis*, 307; *holmgrenii*, 307; *hospitalis*, 307; *huigrensis*, 308; *kalbreyeri*, 308; *lasiantha*, 308; *levis*, 308; *lugubris*, 308; *oreadium*, 308; *pasti*, 308  
*Panicum deustum*, 207  
*Panus laevis*, 168; *rudis*, 168; *stipticus*, 174; *strigosus*, 168  
*Paraleucobryum longifolium*, 512  
*Parmelia caperata*, 161; *cladonia*, 163; *conspersa*, 163; *physodes*, 161-164; *ru-decta*, 163  
*Paspalum commersonii*, 212; *dilatatum*, 212; *orbiculare*, 212  
*Paxillus involutus*, 174  
*Pelargonium zonale*, 566  
*Pellaea gracilis*, 418; *hastata*, 419; *nitidula*, 419; *stelleri*, 418  
*Peltigera variolosa*, 163  
*Penicillium luteum*, 361; *notatum*, 165, 179, 182-184, 188, 189, 361-365  
*Peniophora allescheri*, 168; *cinerea*, 169, 170; *coccineofulva*, 169; *gigantea*, 168; *incarnata*, 169, 170; *nuda*, 169; *pubera*, 168  
*Pennisetum polystachyum*, 206  
*Phacopsora apoda*, 206; *desmum*, 206; *greweae*, 206, 210, 211; *hansfordii*, 205; *stereospermi*, 205  
*Phegopteris distans*, 426; *erubescens*, 408; *hexagonoptera*, 411; *punctata*, 411; *robertiana*, 410; *vulgaris*, 410  
*Philonotis americana*, 514; *fontana*, 514  
*Phymatodes stracheyi*, 423  
*Phlebia strigosozonata*, 180, 186  
*Pholiota adiposa*, 166, 168; *aeruginosa*, 175; *aurivella*, 168; *limonella*, 168; *lutea*, 169; *spectabilis*, 168, 169  
*Phragmopyxis leonensis*, 216, 217  
*Phycomyces blakesleeana*, 76-85, 166  
*Phyllanthus discoides*, 207, 221  
*Physcia* sp., 163  
*Physcomitrium turbinatum*, 513  
*Phytophthora cinnamomi*, 166  
*Pinus excelsa*, 399; *longifolia*, 399, 422  
*Pistia stratiotes*, 87  
*Pisum sativum*, 573  
*Plagiochila ludoviciana*, 508, 510  
*Plagiothecium denticulatum*, 517; *deplanatum*, 517; *elegans*, 518; *laetum*, 518; *muellerianum*, 518; *roseanum*, 518; *sylvaticum*, 518; *turfaceum*, 518  
*Plectocolea crenulata*, 510  
*Pleopeltis clathrata*, 424; *membranacea*, 423; *stewartii*, 423  
*Pleurotus corticatus*, 168; *griseus*, 175, 180-189; *ostreatus*, 168; *sapidus*, 168; *ulmarius*, 168  
*Pleurozium schreberi*, 516  
*Podophyllum diphyllum*, 270

- Pogonatum pensilvanicum*, 519  
*Pohlia cruda*, 513; *nutans*, 513  
*Polycodium melanocarpum*, 2; *stamineum*, 2  
*Polypodium aculeatum*, 412; *africanum*, 409; *argutum*, 401, 423; *aristatum*, 413; *brunneum*, 426; *calcareum*, 410; *clathratum*, 423, 424; *crenatum*, 407; *dentatum*, 409; *dentigerum*, 415; *distans*, 426; *erubescens*, 408; *excavatum*, 423, 424; *filix-femina*, 414; *filix-mas*, 405; *fontanum*, 417; *fragile*, 414; *fragrans*, 420; *hexagonopterum*, 411; *lachnopus*, 401, 423; *latrepens*, 400, 409; *lineare*, 402; var. *loriforme*, 423; var. *steniste*, 423; *lineatum*, 406; *lonchitis*, 411; *loriforme*, 402, 423, 424; *membranaceum*, 403, 423; *microrrhizoma*, 401, 422; *montanum*, 404; *phlegopteris*, 410; *porosum*, 424; *proliferum*, 409; *pteridioides*, 420; *punctatum*, 411; *robertianum*, 410; *stewartii*, 423; *stracheyi*, 401, 423  
*Polypogon alopecuroides*, 544; *monspeliensis* var. *monolepis*, 544  
*Polyporus abietinus*, 168; *albellus*, 175, 180; *alboluteus*, 175; *adustus*, 168; *anceps*, 168, 188; *arcularius*, 168; *balsameus*, 175; *berkeleyi*, 168; *betulinus*, 175; *biformis*, 175, 180; *borealis*, 169; *brumalis*, 168; *cinnebarinus*, 168; *circinatus*, 169; *compactus*, 169; *cristatus*, 169; *croceus*, 169; *curtisii*, 169; *cuticularis*, 168; *delectans*, 175, 180; *dichrous*, 168; *distortus*, 168; *dryadeus*, 168; *dryophilus*, 168; var. *vulpinus*, 169; *durescens*, 175; *ectypus*, 168; *fibrillosus*, 168; *fixilis*, 168; *fragilis*, 175; *frondosus*, 168; *fumidiceps*, 175; *fumosus*, 168; *galactinus*, 175; *giganteus*, 175, 180, 187; *gilvus*, 168; *glomeratus*, 168; *graveolens*, 168; *guttulatus*, 175; *hirsutus*, 168; *hispidus*, 168; *hydroides*, 168; *immitus*, 175; *lucidus*, 168; *ludovicianus*, 169; *mutabilis*, 168; *obtusus*, 175, 180; *oregonensis*, 169; *osseus*, 169; *palustris*, 176; *pargamenus*, 168, 169; *picipes*, 168; *pinsitus*, 168; *pubescens*, 168; *radiatus*, 176, 180; *resinosus*, 168, 176, 180; *robiniophilus*, 168; *rutilans*, 168; *schweinitzii*, 169, 170, 176, 180; *spraguei*, 169, 170; *spumeus*, 168; var. *malicola*, 168; *squamosus*, 168; *subcartilagineus*, 176; *subectypus*, 168; *sulphureus*, 169; *suptinus*, 168; *tenuis*, 168; *texanus*, 168; *trabeus*, 176, 180; *tuberaster*, 169; *tuckahoe*, 169; *tulpiferus*, 176, 179; *varius*, 169; *velutinus*, 168; *versicolor*, 166, 168; *volvatus*, 169; *vulpinus*, 176, 179; *zonalis*, 168; *zonatus*, 168  
*Polystichum aculeatum*, 402, 412, 413; var. *rufobarbatum*, 412; *angulare*, 412, 413; *aristatum*, 401, 413; *bakerianum*, 412; *falcatum*, 413; subsp. *caryotideum*, 413; *lachenense*, 411; *lonchitis*, 411; *prescottianum*, 411, 412; var. *bakerianum*, 412; *squarrosus*, 412; *thomsoni*, 411, 412; *tsus-simense*, 412  
*Polytrichum commune*, 519; *juniperinum*, 519; *ohioense*, 519; *piliferum*, 508, 519  
*Porella pinnata*, 510; *platyphylloidea*, 510  
*Porotrichum alleghaniense*, 514  
*Poria ambigua*, 168; *andersonii*, 169; *carbonica*, 169, 170; *cocos*, 176; *colorea*, 176; *corticola*, 176, 180, 182, 183, 187, 188; *ferrea*, 176; *ferruginea-fusca*, 176, 180, 187; *ferruginosa*, 168, 169; *incrasata*, 176, 179, 189; *inermis*, 168; *inflata*, 169; *luteofibrata*, 170, 171, 176; *microscopora*, 177; *mutans*, 168; *nigra*, 177; *nigrescens*, 168; *obliqua*, 168; *prunicola*, 168, 169; *punctata*, 169; *sequoiae*, 177, 180; *spiculosa*, 168; *subacida*, 177, 180, 183, 184, 187, 188; *tenuis*, 177, 181, 182, 184, 187, 188; *vaillantii*, 177; *vaporaria*, 177; *weirii*, 168, 177; *xantha*, 177  
*Portulaca*, 22; *cyanosperma*, 24  
*Posoqueria latifolia*, 309  
*Prosnierpis panamensis*, 478  
*Proteus vulgaris*, 158, 161, 163  
*Prunus avium*, 137, 149-156; *mahaleb*, 149; *pennsylvanica*, 149; *persica*, 137-151, 155, 156; *serotina*, 149; *virginiana*, 149  
*Psychotria brachiata*, 309; *bullatifolia*, 309; *cuspidata*, 309; *hartwegiana*, 309; *hirta*, 309; *jamesoniana*, 309; *lateriflora*, 309; *macrophylla*, 309; *patens*, 309; *pilosa*, 309; *recordiana*, 309; *rimbachii*, 309; *rufescens*, 309; *tenuifolia*, 309  
*Pteridium aquilinum*, 402; var. *wightianum*, 422  
*Pteris aquilina*, 422; *biaurita*, 422; var. *quadriaurita*, 422; *calomelanos*, 419; *cretica*, 402, 422; *excelsa*, 422; *farinosa*, 421; *hastata*, 419; *longifolia*, 402, 422; *nitidula*, 419; *quadriaurita*, 422; *stelleri*, 418; *vittata*, 422  
*Ptilanthus*, 472; *scandens*, 472  
*Ptilidium ciliare*, 507, 509; *pulcherrimum*, 509  
*Ptychogaster cubensis*, 168; *rubescens*, 177  
*Puccinia andropogonicola*, 209, 211; *andropogonis-micranthi*, 211; *cacao*, 211; *caraacasana*, 213; *cesatii*, 209; *chaetochloae*,

- 212; *dolosa*, 212; *dolosoides*, 209-212; *incompleta*, 209; *kampalensis*, 211; *kenmorensis*, 209, 211; *minussensis*, 214; var. *africana*, 213; *nanishikii*, 209; *paspalina*, 211, 212, 217; *penniseti*, 213; *propinqua*, 209; *scleriae*, 213; *stenotaphri*, 213; *substriata*, 212  
*Puccinosira deightonii*, 218  
*Pylaia intricata*, 511; *selwynii*, 511  
*Pythiomorpha gonapodydes*, 166  
*Pythium butleri*, 166; *helicoides*, 166
- Quercus incana*, 406
- Radula complanata*, 510; *obconica*, 510  
*Radulum orbiculare*, 177, 180, 186, 187  
*Ravenellii bottomleyae*, 215; *hansfordii*, 214, 215; *laevioidea*, 215; *maranguensis*, 211, 215  
*Reboulia hemisphaerica*, 511  
*Relbunium ciliatum*, 310; *hirsutum*, 310; *hypocarpum*, 311; *nitidum*, 311  
*Remijia pedunculata*, 464  
Report of some recent collections of Rubiaceae from Ecuador, 295  
*Rhacomitrium heterostichum* var. *gracilescens*, 508, 513  
*Rhabdoweisia denticulata*, 512  
*Elizidiomyces apophysatus*, 47, 48; *bivelatus*, 47, 48, 50; *hansonae*, 47, 48; *hirsutus* sp. nov., a hairy anisochytrid from Brazil, 47  
*Rhizopus nigricans*, 166  
*Rhodobryum roseum*, 513  
*Rhytidadelphus triquetrus*, 519  
*Rhytidium rugosum*, 519  
*Ricinus communis*, 566  
*Ribes odoratissimum*, 263  
RICKETT, H. W., New combinations in *Cornus*, 223  
RILEY, HERBERT PARKES, Inheritance of orange and yellow flower color in *Nemesia strumosa*, 435  
ROBBINS, WILLIAM, C., A survey of some wood-destroying and other fungi for antibacterial activity, 165  
ROBINS, WILLIAM J., A survey of some wood-destroying and other fungi for antibacterial activity, 165; Effect of cotton on the germination of phycomyces spores, 76  
*Rondeletia trichotoma*, 311  
*Roraimanthus imthurnianus*, 528  
Rubiaceae, report of some recent collections from Ecuador, 295  
*Rubus odoratus*, 349  
*Rudgea cornifolia*, 311; *fimbriata*, 311  
Rusts, tropical, 205-222
- Sabicea paraensis*, 311; *villosa*, 311  
*Salvinia natans*, 424  
*Sapota sideroxydon*, 556  
Sapotaceae, studies in, 191, 550  
*Sarcina lutea*, 158-161, 163  
*Sauvagea*, 521-540; *adima*, 528, 529; *amoena*, 526, 534, 535, 538; *angustifolia*, 522, 532; *brownei*, 523, 525, 527; *deficiens*, 522, 526, 536, 537; *deflexifolia*, 526, 538, 539; *duckei*, 533; *elata*, 526, 531; *erecta*, 523, 525-532; *fruticosa*, 522, 532; *geminiflora*, 529; *gracilis*, 539; *grandifolia*, 526, 530; *imthurniana*, 526, 528, 539; *inconspicua*, 539; *kapleri*, 532; *laza*, 529; *linearifolia*, 526, 537, 538; *longifolia*, 524, 526, 534; *microphylla*, 526, 527; *nana*, 539; *nutans*, 528; *peruviana*, 528; *pulchella*, 526, 539; *pusilla*, 537; *racemosa*, 526, 532; *ramosissima*, 526, 535; *rosea*, 532, 533; *rubiginosa*, 529; *serpyllifolia*, 532; *smithiana*, 522, 524, 526, 536, 537; *sprengelii*, 522, 523, 526, 532, 534; *stenophylla*, 526, 527; *striata*, 533; *tenella*, 523, 524, 526, 539  
*Schizophyllum commune*, 166, 168  
SCHMITT, MARY BARTLEY, Effect of cotton on the germination of *Phycomyces* spores, 76  
SCHNEIDER, HENRY, The anatomy of peach and cherry phloem, 137  
SCHNOOBERGER, IRMA, The bryophytes of Shenandoah National Park, Virginia, 506  
*Schwetsckheopsis denticulata*, 515  
*Sciaromium lescurei*, 516  
*Scilla campanulata*, 573  
*Scleria melanomphala*, 218; *naumanniana*, 213  
*Sclerotium delphini*, 166; *rolfsii*, 166  
*Scopania undulata*, 510  
*Sedum beyrichianum*, 376; *nevei*, 376; *nutallianum*, 375; *pulchellum*, 375-377; *ternatum*, 376  
*Selaginella aitchisoni*, 426; *borealis*, 426; *jaquemontii*, 426; *sanguinolenta*, 426  
*Sematophyllum caespitosum*, 508, 518; *carolinianum*, 518; *marylandicum*, 518  
*Serratia marcescens*, 158, 161  
*Setaria aequalis*, 206; *pallida-fusca*, 207; *rubiginosa*, 207; *verticillata*, 207  
*Shaferodendron mayarensis*, 558; *moensis*, 558, 559  
Shoot of *Botrychium* interpreted as a series of dichotomies, 491

- Sloanea emarginata*, 557  
*Solanum anomalum*, 212  
*Solidago*, genes in, 235-244; *rugosa*, 237, 238; var. *typica*, 237, 243; *sempervirens*, 237-243; subsp. *mexicana*, 241; subsp. *typica*, 241; var. *mexicana*, 237, 239, 243; var. *typica*, 237, 239, 243  
Some Melastomaceae of Colombia, 472  
*Sparassis crispa*, 177  
*Sphaerophorus globosus*, 163  
*Sphaerophragmium acaciae*, 216  
*Sphenospora mera*, 214  
*Sporotrichum globulium*, 166  
*Staphylococcus albus*, 158, 161; *aureus*, 158, 160-189  
ST. JOHN, HAROLD, *Dryopteris*, *Deschampsia*, *Portulaca*, *Lupinus*, *Fagara*, *Stenogyne*, and *Dubautia*. Hawaiian plant studies 12, 22  
STEERE, WILLIAM CAMPBELL, A report of some recent collections of Rubiaceae from Ecuador, 295; The discovery and distribution of *Cinchona pitayensis* in Ecuador, 464  
*Stenogyne*, 22; *kaalae*, 25; var. *coriacea*, 25; *mollis*, 25; *rugosa*, 25, 26; var. *mollis*, 25; var. *subulata*, 25  
*Stenotaphrum dimidiatum*, 213  
*Stereocaulon paschale*, 161  
*Stereum albobadium*, 168; *fasciatum*, 177; *frustulosum*, 169; *fusum*, 177; *gausapatum*, 177, 180, 186; *hirsutum*, 168; *ochraceoflavum*, 168; *murrayi*, 166, 179, 180; *pini*, 168; *purpureum*, 168; *rameale*, 169; *roseo-carnum*, 168; *rufum*, 169; *rugosum*, 178, 180, 187; *sanguinolentum*, 168, 169; *sericeum*, 169; *spadiceum*, 168; *subpileatum*, 178; *sulcatum*, 178, 180, 187  
STEWART, RALPH R., The ferns of Kashmir, 399  
*Streptococcus haemolyticus*, 158, 161; *viridans*, 158, 161  
Studies in the Sapotaceae—I. The North American species of *Chrysophyllum*, 191; IV. The North American species of *Manilkara*, 550  
Survey of some wood-destroying and other fungi for antibacterial activity, 165  
*Symphoricarpos leucocarpus*, 263  
*Syngamme fraxinea*, 419; *vestita*, 418  
TART, CLARENCE E., The validity of the algal genus *Thamniastrum*, 246  
Taxonomy of the genus *Sauvagesia* (Ochnaceae), 521  
*Tetraphis pellucida*, 513  
*Thamniastrum*, the genus, 246  
*Thamnia vermicularis*, 163  
*Thelia asprella*, 515; *hirtella*, 515  
Thomas Jefferson, his interest in plant life as revealed in his writings—II, 248  
*Thuidium abietinum*, 515; *delicatulum*, 515; *philiberti*, 508, 515; *recognitum*, 515; *scitum*, 515; *virginianum*, 516  
Tobacco, glandular leaf-hairs of, 345  
*Todea barbara*, 500  
*Topobea*, 385; *alternifolia*, 390; *barbata*, 393; *longisepala*, 392; *pubescens*, 392; *stephanochaeta*, 392  
*Tortella caespitosa*, 512  
*Trametes alaskanae*, 178; *americana*, 178; *carnea*, 178; *cubensis*, 168; *heteromorpha*, 178; *hispida*, 168; *malicola*, 178; *rigida*, 168; *rubescens*, 178, 180, 187; *sepium*, 178; *serialis*, 178; *suaveolens*, 168  
*Trichophyton crateriforme*, 171; *gypseum*, 166; *interdigitale*, 171; *mentagrophytes*, 171; *purpureum*, 178; *rosaceum*, 171; *tonsurans*, 171; *violaceum*, 171  
Tropical rusts, 205-222  
*Tyleria floribunda*, 523  
*Uloa americana*, 514; *crispa*, 514  
*Umbilicaria dillenii*, 163; *papulosa*, 163  
*Uredo achyranthicola*, 219; *achyranthis*, 219; *arundinella-e-nepalensis*, 218; *brachylaenae*, 221; *corbiculoides*, 206, 211, 219, 220; *crassiperidiata*, 218; *diocleae*, 219; *elephantopodis*, 221; *famelica*, 219; *gossypii*, 206; *grewii*, 220; *longaensis*, 220; *maranguensis*, 215, 216; *melinidis*, 207; *mira*, 211; *palpigera*, 221; *paspalina*, 212; *pergulariae*, 220; *perscitra*, 220, 221; *stenoptaphri*, 213; *stereospermi*, 205; *toroiana*, 220, 221; *vernonicola*, 220, 221  
*Uromyces aspillicola*, 208, 217; *baccarinii*, 208; *leptodermus*, 207; *pretoriensis*, 208; *schinzianus*, 208, 211  
*Urostigma altissimum*, 394, 396; *lacciferum*, 294, 397  
*Urtica dioica*, 349  
*Usnea florida*, 161, 164  
*Vaccinium* hybrids and the development of new horticultural material, 1; *altomontanum*, 3, 7, 16; *amoenum*, 3, 8; *angustifolium*, 3, 6, 11, 18; *arctostaphylos*, 3; *arkansanum*, 3, 7, 8; *ashei*, 3, 4, 8, 16-19; *atrococcum*, 2, 4-6, 11, 19, 46; *australe*, 3, 4, 6, 7, 8, 19; *brittonii*, 3, 6, 7, 11; *caesariense*, 5, 6; *constablaei*, 3, 4; *corymbosum*, 3, 6, 7, 9, 11; *cuthbertii*, 5; *darrowi*, 2, 4, 5, 12; *elliottii*, 3-6, 12;

- fuscatum*, 8; *hirsutum*, 3; *lamarckii*, 3, 4, 6, 7, 11; *macrocarpum*, 1; *marginarettae*, 5; *marianum*, 6, 7; *missouriense*, 5; *myrsinites*, 3, 4, 7, 8, 18, 19; *myrtilloides*, 2, 3, 6, 16, 17; *ovatum*, 3; *pallidum*, 2, 3, 5, 18; *simulatum*, 3, 7; *tallapusae*, 3, 4, 7, 18; *tenellum*, 2-5, 8, 12; *torreyanum*, 46; *uliginosum*, 1; *vacillans*, 5, 6, 11; var. *crinitum*, 5; *virgatum*, 3, 4, 8, 16
- Validity of the algal genus *Thamniastrum*, 246
- Variations and origin of *Botrychium lanuginosum*, 454
- Varinga latifolia*, 394, 396, 398
- Vernonia amygdalina*, 220
- Verticillium buxi*, 168
- Vicia faba*, 569, 570
- Volutella buxi*, 168
- Volvox*, morphological and cytological study of a new form of, —I, 86; II, 121; *africanus*, 89, 90, 132; *aureus*, 88, 89, 104, 106, 121, 125, 128; *capensis*, 89, 107; *carteri*, 86-113, 121-134; var. *hazeni*, 111, 129, 130, 132, 134; var. *homothallicus*, 132, 134; var. *weismannia*, 128; f. *magariensis*, 129; *gigas*, 89, 99, 132; *globator*, 88, 89, 104, 128; *migulae*, 132, 134; *minor*, 88, 121; *mononae*, 128, 132, 134; *obversus*, 131, 132; *perglobator*, 104, 128; *rousselletii*, 89, 106, 107, 113; *spermatosphaera*, 128; *tertius*, 89-91, 99, 104, 106, 129, 132, 133; *weismannia*, 128, 129, 132
- Wedelia oblonga*, 213
- Weisia viridula*, 512
- WOLF, F. A., Glandular leaf-hairs of Oriental tobacco, 345
- Wood-destroying fungi, 166-189
- Woodsia alpina*, 402, 404; *hyperborea*, 404
- Woodwardia radicans*, 401, 408, 418
- WYNNE, FRANCES E., The bryophytes of Shenandoah National Park, Virginia, 506
- X-rays, effect of on plant tissue, 566, 567, 572, 573
- Xanthoria parietina*, 163, 164
- Xanthoxylum dipetalum* var. *geminicarpum*, 24; *mauiense* var. *anceps* f. *petiolulatum*, 25
- Zimapania schiedeana*, 37



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